DEVELOPMENT OF AN ALTRICIAL MARINE MAMMAL AT SEA: ACTIVITY AND ENERGY BUDGETS OF FEMALE SEA OTTERS AND THEIR PUPS IN SIMPSON BAY, ALASKA

A Dissertation

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ABSTRACT

Sea otters are the most altricial marine mammal born at sea. Female sea otters not only protect the pup from environmental and predatory threats, but also provide energy for pup activity and growth while simultaneously supporting their own elevated metabolism throughout lactation. The behavior of female sea otters and their pups was recorded during the first three months postpartum in Simpson Bay, Alaska and compiled to produce simultaneous 24-h activity budgets. Energy budgets were created from the activity budgets and published metabolic rates for certain behaviors of captive sea otters. Pups were classified into three behavioral/size categories: Category 1 (C1) 0-<4 wk old; Category 2 (C2) 4-<8 wk old; Category 3 (C3) 8-12 wk.

Energy associated with activity ($Energy_{activity}$) for all females was similar regardless of pup age (range: 10.79-11.03 MJ day^{-1}). However, the C1 females allocated more time and energy to grooming behaviors and swimming, while C3 female allocated more time and energy to feeding. The time females spent feeding increased from 9% (C1) to 32% (C3). Energy associated with lactation ($Energy_{lactation}$) increased 3.5-fold, while daily food ingestion increased from 29% to 39% for C1 to C3 females (mean body mass: 20 kg).

Energy for pup growth ($Energy_{growth}$) increased 2.28-fold, while the $Energy_{activity}$ increased 3.5-fold from C1 to C3 pups. C1 pups spent 83% of their day resting, which decreased to 48% for C3 pups. Time spent nursing remained constant (ca. 8%) for all pup categories, but feeding on solid food provided mainly by the female increased to

17% (C3 pups). Daily milk ingestion regardless of pup age was 7-8% of mean body mass. Our results provide a quantitative picture of the changes in female and pup behavioral patterns and energy output during the critical developmental stages. Our study revealed the energetic strategies that female sea otters use to support one of the highest metabolic rates in any adult and neonatal carnivore. These energy budgets also reflected the extreme energetic demands placed on female sea otters while caring for developing altricial pups at sea.

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INTRODUCTION

1.1 Parental Care in Mammals

Parental investment increases survival of offspring but is associated with substantial costs to the female (i.e. an energetic expenditure for milk production and thermoregulation, in addition to an increased risk of predation and limited mobility resulting from the presence of neonates), which may affect her ability to invest in future offspring (Zeveloff and Boyce, 1980; Nowak et al., 2000). Parents must decide between investing resources into their own fitness, which ensures future reproductive success, or investing resources into the current offspring (Parent-Offspring Conflict) (Gonzalez-Voyer and Kolm, 2010). If the cost of sustaining the current offspring exceeds the benefits, the parent will dissociate with the offspring, which usually entails weaning (Gonzalez-Voyer, 2010). As parents, there is an obligation by the female to provide energy to the offspring for a set period of time (Case, 1978a). Females generally spend 80% of her life attending to young (Gittleman, 1994). Although all female mammals supply milk to their young, the duration of lactation varies across species (Lefèvre et al., 2010; Balshine, 2012). Lactation length in some phocids (Family Phocidae) can be as little as 4 or 5 days, while chimpanzees and orangutans can have lactation lengths of over 900 days (Lefèvre et al., 2010).

Female mammals care for young alone or with the assistance of the male, kin or communal members (Balshine, 2012). Three general forms of parental care are found

among mammals. Solitary care, where females raise young without the support of males or other adult helpers, is the predominant form of mammalian parental care (Gittleman, 1994). Female mammals generally spend 80% of her life attending to young (Gittleman, 1994), Sea otters utilize this form of parental care, as well as some primates and all ursids (Gittleman, 1994). In biparental care systems, the females provide care to her young similarly to the solitary care systems. However, she receives assistance from an attendant male who provides solid food, protection, and cares for young as much as the female (Gittleman, 1994). This type of care occurs in 9-10% of mammalian genera, including many canids (Family Canidae) and the marine otter (*Lontra felina*) (Gittleman, 1994; Balshine, 2012). Solitary female care is more primitive while biparental care is derived (Balshine, 2012). In communal systems, multiple males and/or females assist a mother, such as in wolves or lions (Gittleman, 1994). Biparental and communal systems allow for a significant reduction in time and energy feeding, guarding, and attending to the young (Gittleman, 1994). The adult assistants may be older offspring, which indirectly benefit from providing care by ensuring the survival of shared genes and gaining experience in parental care (Gonzalez-Voyer and Kolm, 2010). Solitary parental care is the most costly system for the female, because she must provide everything for the young.

1.2 Sea Otter Reproduction

Although sea otters in Prince William Sound show peak breeding in the autumn, breeding occurs throughout the year (Finerty et al., 2009). Adult males enter areas

preferred by females and establish territories from spring to autumn in a reproductive strategy called resource-defense polygyny (Monnett et al., 1991; Finerty et al., 2009). Females reach sexual maturity between three to five years of age (Monson, 2000) and usually give birth to one pup during early spring, which minimizes the energetic demands from inclement weather (Jameson and Jameson, 1993). Since male sea otters do not participate in pup rearing, the female uses the solitary strategy of parental care and this incurs a cost (i.e., increased foraging, reduced body condition, increased vulnerability to predation) in terms of her survival and the ability to successfully rear future offspring (Trivers 1974; Zeveloff and Boyce 1980). Reproductive effort was defined by Millar (1977) as the amount of energy required by a female (relative to the requirements of a nonbreeding female) to support offspring until weaning when their metabolic requirements are greatest. Female reproductive effort accounts for energetic expenditure from gestation to weaning (Millar 1977; Beck et al., 2003; Gittleman and Thomson 1988).

During gestation, the female provides all the energy necessary for production of fetal, placental and mammary tissue, with peak energy production typically occurring a few days prior to parturition (Gittleman and Thompson 1988). The offspring of eutherian marine mammals (there are no metatherian marine mammals) derive all their energy from the female though the placenta (Langer 2008). Typical gestation period for sea otters is six months (Jameson and Johnson 1993). To avoid raising a pup in unfavorable environmental conditions, sea otters, like American river otters, display evidence for delayed implantation (Kenyon 1969). After the egg is fertilized, the blastocyst enters a

period of rest for 2- 3 mo. until ready for implantation in the uterine horn resulting in fetal growth (Kenyon 1969; Jameson and Johnson 1993). The last 4 mo. of the gestation period is the implanted phase (Jameson and Johnson 1993). The mean body mass and standard length of a sea otter pup at birth is about 2 kg and 60 cm, respectively (Kenyon, 1969; Monnett et al., 1991).

After birth, milk via female lactation provides energy for neonatal thermogenesis, activity and growth until the offspring is fully weaned. It is this critical period of reproduction that is energetically expensive for the female and the most susceptible to failure, resulting in loss of the offspring (Millar, 1977; Costa et al., 1986; Costa and Gentry, 1986; Jenness, 1986; Gittleman and Oftedal, 1987; Gittleman and Thompson, 1988; Boyd, 1998; Rogowitz, 1996; Gamel et al., 2005). A three-fold increase in energy expenditure from gestation to lactation may be required, and maintenance metabolic rates can be 66-266% higher than that of a non-breeding female (Gittleman and Thompson, 1988; Rogowitz, 1996; Costa et al., 1986). A large percentage of energy required for reproduction is allocated to milk production (Gittleman and Oftedal, 1987), which provides the offspring with energy, amino acids, antibodies, and other vitamins and minerals necessary for growth and development (Jenness, 1986). In most canids, pairs or groups defend a territory and all adults help defend and provide food for the young and may even provide food for the female (Malcolm, 1985). However, most mammalian females raise young without the help of males or other adult helpers (Gittleman, 1994), and the females must incur this elevated cost of lactation on their own. Females can compensate for an increase in energetic

demand during lactation by mobilizing energy stores (mainly fat) or increasing food consumption (Gittleman and Thompson, 1988; Rogowitz, 1996; Mellish et al., 2000; Bowen et al., 2001). The particular compensatory strategy used will have an impact on the growth and development of the offspring (Burns, 2004).

The most common compensation method for increased energetic demands from lactation is to increase food intake, which can be 1.7 to 2.9 times greater than that of non-lactating females (Costa et al., 1986; Gittleman and Thompson, 1988; Rogowitz, 1996; Mellish et al., 2000). Many otariids (Family Otariidae) exhibit an income-based foraging strategy, where they feed throughout a long lactation period, and produce milk with a lower lipid (17-45%) and energy content (Costa et al., 1986; Bonness and Bowen, 1996; Burns, 2004; Gamel et al., 2005). This income based compensatory strategy allows for the gradual formation of lean tissue rather than a blubber layer in pups (Burns, 2004; Gamel et al., 2005) and thus, reduces loss of body mass in the female (Skiebel et al., 2013).

Among marine mammals, seals and baleen whales (Order Cetacea, Suborder Mysticeti) will reduce activity and thermoregulatory costs and rely on internal energy reserves (e.g., blubber) to support lactation until offspring are weaned (Gittleman and Thompson, 1988; Bonnet et al., 1998; Boyd, 1998; Beck et al., 2003; Skiebel et al., 2013). This strategy is referred to as capital breeding in which feeding and reproduction are spatially and temporarily separated and include a fasting period during offspring development. Mammals that use a fasting compensatory strategy produce milk with low carbohydrate and high fat concentrations (Oftedal, 2000). For example, phocids usually

rely on a rapid weaning strategy and supply their offspring with milk that has a high fat content (25-60%) leading to a rapid formation of adipose tissue in the young (Bonness and Bowen, 1996; Gamel et al., 2005). This lowers the metabolic overhead of the female allowing for a greater energy transfer to the offspring (Boyd, 1998). The fasting strategy has a higher *daily* milk energy output, while the foraging strategy has a higher *total* milk energy output due to the longer lactation period (Boness and Bowen, 1996). Smaller mammals, like sea otters, expend energy at a higher rate than larger mammals, and therefore have limited energy reserves (Oftedal, 2000). Therefore, capital breeding is more efficient in larger mammals.

The most influential and unique variable of mammalian reproduction is the production of milk (Gittleman and Thompson, 1988). The early stage of lactation is the milk-only phase, where the offspring are entirely dependent on the females' milk (Langer, 2008). The second phase of lactation is the complementary feeding phase in which energy requirements of the young mammal cannot be sustained solely by milk and must be supplemented with solid food (Langer 2008). At weaning, which may be abrupt or last months to years, the young transitions from milk to solid food (Langer, 2008). Lactation is a critical stage in pup rearing, however weaning is of interest to the females rather than the young (i.e., maternal offspring conflict) (Langer, 2008). As the energetic demand from the pups increases, the females may provide less energy than is physiologically needed by the pup (i.e., pup begins to forage on its own) to ensure her own reproductive success (Monson, 2000). At weaning, the young have achieved an adult degree of independence and are capable of acquiring resources on their own

(Galef, 1981). The weaning mass of young may influence survival and also serve as indicators of total maternal effort (Lee, 1991). In species such as sea otters in Prince William Sound that gradually wean their pups over ca. six months (Monnett and Rotterman, 2000), the female provides both milk and solid food for the physiologically immature (in terms of diving and foraging ability) and inexperienced young.

1.3 Sea Otter Ecology

The resting metabolism of sea otters is 2-3 times higher than that of similar-size terrestrial mammals, and they must consume about 25% of their body weight in food each day (Kenyon, 1969; Osterreider and Davis, 2009; Finerty et al., 2009; Yeates et al., 2007). Sea otters are opportunistic foragers, and their diet depends on prey availability (Green and Brueggeman, 1991). They use their forepaws to gather food, hence the belief that the tactile sense is important during foraging. The vibrissae, which are sensory bristles on the muzzle, may also serve an important function in locating food (Kenyon, 1969). Sea otter vibrissae are located rostrally leading to the belief that they are important in identifying epibenthic prey items, which is consistent in other benthic feeders such as walruses (Marshall et al., 2014). They are also highly innervated, which may allow for levels of sensitivity comparable to that of harbor seals or California sea lions (Marshall et al., 2014). A sea otter diet usually consists of benthic invertebrates and, at times, finfish. Individual otters may exhibit food specialization by favoring a certain prey item (Tinker et al., 2007). During a foraging bout, food is brought to the surface and consumed (Kenyon, 1969). Due to their easy access and high energy

content, mussels appear to form a large part of the diet of young otters, females with dependent pups, and animals in poor health (Green and Brueggeman, 1991).

Unlike most marine mammals that have a blubber layer for insulation in water, sea otters rely on fur for thermal insulation and their elevated resting metabolic rate to maintain a stable core body temperature of ca. 37^{o} typical of most mammals (Kenyon 1975; Costa 1982; Costa and Kooyman 1982; Willams et al., 1992). The other exclusively marine otter, *Lontra felina*, has no body fat like the sea otter, however they offset heat loss by reducing the time spent in the water (Vianna et al., 2010; Valqui, 2012). More than 80% of their time is spent in the dens and mainly only go to the water to feed (Vianna et al., 2010; Valqui, 2012). Sea otter hair follicles have many fine underhairs and one, large guard hair resulting in a pelage density that may reach 26,000 to 165,000 hairs per cm^{-2} depending on the region of the body (Williams et al., 1992). Normal grooming behavior consists of active felting and aerating of the fur layer to maintain an air layer adjacent to the skin, which provides 70% of the thermal insulation (Kenyon 1975; Costa and Kooyman 1982; Davis et al., 1988; Williams et al., 1992).

1.4 Mammalian Growth

In terms of the energetic needs of the young mammals from conception to weaning, the young must balance energetic demands from lean tissue synthesis and body growth, lipid storage, and any energetic expenditure for activity, while acquiring energy solely from the female (Arnould et al., 2003). Neonatal growth from new tissue synthesis is greater than during any other stage of development (Davis et al., 2008) and requires energy,

protein, calcium and other macronutrients (Speakman, 2008). There are many factors that influence growth rate, including precociality/altriciality, brain size, birth weight and feeding habits (Case, 1978b). Some pinnipeds, cetaceans, and canids have the highest growth rates and efficiencies, whereas other aquatic species and most other fissiped carnivores grow at more moderate rates. The fastest relative growth rates have been recorded in seals, with young ribbon and harbor seal pups growing at rates 70-fold greater than human infants (Case, 1978b).

Alaskan sea otter pups grow at a faster rate than pups born along the California coast, which might explain the higher survival rate of Alaskan pups (Riedman et al., 1994). Furthermore, male pups tend to gain mass faster than female pups. This may stem from male pups being capable of consuming solid food at an earlier age or a genetic predisposition (Monnett et al., 1991). Growth rates from birth to weaning of wild sea otter pups in Prince William Sound averages 95 g day^{-1} for male pups and 83 g day^{-1} for females (Monnett et al., 1991).

The amount of time and energy that a parent invests differs depending on whether the offspring are altricial or precocial. Altricial offspring are immature, helpless and require postnatal care for an extended period of time as the young develops the skills necessary for survival (i.e. canids, felids, most rodents and lagomorphs) (Künkele and Trillmich, 1997; Nowak et al., 2000; Langer, 2008). Altriciality is characterized by rapid prenatal development that is not as energetically costly and provides the female with the option of sharing postnatal costs with a male or kin alleviating the increased expenditure to the female (Case, 1978a). They typically have smaller brains (10% of adult size;

Grand, 1992) and weakly developed muscles at birth due to the shorter gestation time (Langer, 2008). Altricial young are favored in species that spend greater amounts of time and energy searching for food, such as in certain carnivores. The young regardless of maturity would not be capable of complex hunting behaviors and would not be capable of hunting with the female (Case, 1978a). In addition, carrying large eggs or embryos throughout a prolonged gestation period might interfere with the female's active searching or hunting for prey. Therefore, these females can alleviate constraints by reducing their gestation period and giving birth to an immature offspring. Most mammals produce altricial neonates (Derrickson, 1992), which is true for sea otters.

In contrast, precocial neonates, such as in ungulates and cetaceans, have a greater body mass (i.e., ca. 50% of adult size; Grand 1992) and well developed locomotor and sensory abilities due to longer gestation periods and smaller litter sizes (Hennemann 1984; Derrickson 1992; Künkele and Trillmich 1997; Nowak et al., 2000). Precocial newborn giraffe calves can stand up and run an hour after birth (Pellow, 1984), and by 3-4 weeks can already ingest solid food (Bercovitch et al., 2004). The young are born with a rapid development of inter-individual recognition between themselves and the females, which is especially true in gregarious species (Nowak et al., 2000). Females with precocial young may have an advantage by producing larger offspring that are self-feeding. In species that have easily captured prey, such as ungulates, precocial young would be capable of foraging with the female given that foraging does not require complex hunting skills (Case, 1978a). Offspring in species that have a single precocial offspring typically eat solid food well before weaning, which alleviates the energetic and

nutritional constraints on the female from lactation. The young then benefit more from the female's protection and social and foraging experience rather than provision of milk (Lefèvre et al., 2010). However, dichotomous labeling of the development of neonates is misleading. Instead, it is more realistic to consider offspring development as a continuum (Zeveloff and Boyce, 1980). For example, young may be labeled as an intermediate type whose sensory systems are functional but thermoregulatory capabilities are inefficient, such as pigs, or locomotory capabilities are limited (primates) (Nowak et al., 2000).

1.5 Ecology of Sea Otter Pups

Sea otter pups are the most altricial of marine mammals born at sea being incapable of swimming or diving for the first four to six weeks of life (Kenyon, 1969; Hanson et al., 1993; Osterrieder and Davis, 2011). The female must feed the pup, while protecting it from environmental and predatory threats and maintaining the insulating properties of its fur for thermoregulation. For all mammals, parental care is essential for the early survival of offspring, but this is especially true for neonatal sea otter pups that are completely helpless and, unlike cetaceans and sirenians, cannot swim at birth. The labeling of sea otter pups as altricial is complex, as they have been labeled as precocial in other studies (Case, 1978b; Kenyon, 1969). However the combined inabilities of neonatal sea otters to swim, groom and forage, three critical behaviors essential for survival, make them especially vulnerable to drowning, hypothermia and starvation. The

lack of these behaviors requires the continuous attention of the female, which would make sea otter pups more altricial.

In caring for an altricial pup, female sea otters must support the pup's energetic requirements to cover the resting metabolic rate, which is associated with thermogenesis for thermoregulation, activity and growth. The need to support the pups' high resting metabolism underlies the high cost of lactation for the female (Thompson et al., 1987). Self-grooming behavior, which is essential for thermoregulation, is attempted at a young age (~4-6 weeks) (Payne and Jameson, 1984). However due to the complexity of self-grooming, a pup cannot efficiently groom its entire body until around 8 to 10 weeks (Kenyon, 1969; Payne and Jameson, 1984; Hanson et al., 1993). Pup grooming by females usually entails the female licking the pup's fur, aerating it, and then felting (rubbing) it dry with her forepaws (Kenyon, 1969). By 14-20 weeks, the female rarely grooms the pups, and pups can effectively groom themselves around 5 mo of age.

Newborn pups are often carried on the female's abdomen. When beginning to swim (ca. 3-4 weeks of age), a pup will paddle in an uncoordinated manor and often belly-down (Kenyon, 1969; Payne and Jameson, 1984; Osterrieder and Davis, 2009). Between 4-6 weeks, prone swimming becomes more coordinated, and the pup usually watches the female from the surface as she dives. The pup attempts to dive, however is often unsuccessful due to the buoyancy of the lanugo (Payne and Jameson 1984). Pups begin making shallow dives after 6-10 weeks and must exert additional effort to counteract the positive buoyancy of its air-filled fur (Kenyon, 1969; Payne and Jameson, 1984; Osterrieder and Davis, 2009). Pups attempt swimming in a supine position and

eventually become strong swimmers in the prone and supine positions allowing them to actively dive with the foraging females by around 2 mo. By 3.5 to 5 mos., the females rarely carry the pups (Payne and Jameson, 1984).

In terms of foraging, which is critical for a growing neonate that has an elevated metabolic rate, pups primarily rely on the female's milk the first 6 weeks. The pup solicits an increasing amount of solid food from the female, but are not able to open hard bivalves until around 3.5 mo. Around 5 mo., the pups obtain much of their own food and rarely nurse, yet still solicit food from the female (Payne and Jameson, 1984). Pups are weaned around 6 mo. of age. The weaning period in Prince William Sound usually occurs from September to December (Monnett and Rotterman, 2000). By one year of age, pups are capable of sustaining themselves (Kenyon, 1969). Observational learning may be an important aspect of foraging (Carss, 1995). This has been found to be an important aspect of river otter development as they are seen dropping fish given to them by their mom and recapturing it (Carss, 1995). Observational learning in sea otter pups is represented by their utilization of the same tools that the females utilize to break open invertebrate prey (Mann, 2008).

1.6 Activity and Energy Budgets

Female and offspring go through developmental changes, and this puts a focus on the complementary nature of their changing behavior (Moore, 2007). Sea otter females are ideal for studying maternal care in marine mammals, because most of their behavior occurs at the surface (Sandegreen et al., 1973). Activity and energy budgets are

important for understanding how otters partition resources among different activities, especially during the early (critical) phase of pup growth (Hanson et al., 1993, Monnett and Rotterman, 2000). The changing activity budgets of offspring as they mature indicate the development and acquisition of behaviors and skills critical for independence and survival after weaning. Females must balance their time and energy expenditures between offspring and their own survival (Georges and Guinet 2000). In addition, parental activity and energy budgets serve as an indicator of critical behaviors for rearing offspring, especially in altricial species during early development (Hanson et al., 1993). The female's health is an important factor contributing to the timing of her separation from the pup, which affects pup survival into adulthood (Jameson and Johnson, 1993). The activity budget also indicates whether a population is at equilibrium. Sea otter population size and growth may be regulated by prey abundance (Gregr et al., 2008). Therefore, if a population is approaching carrying capacity, the mean percent of time spent foraging will increase as competition for food increases (Gelatt et al., 2002).

1.7 Conservation Status

Historically, sea otters (*Enhydra lutris*) ranged along the North Pacific Rim from northern Japan to central Baja California with an estimated population of over 300,000. They were hunted to near extinction beginning in the 18th century, and possibly a few thousand or less remained by the early 20th century, mostly as remnant populations in the Aleutian Islands. The North Pacific Fur Seal Treaty of 1911 provided legal protection,

but fewer than 2,000 sea otters remained in thirteen remnant colonies (U.S. Fish and Wildlife Service [USFWS], 2003). Their population gradually increased and expanded throughout their former range, although regional populations remain dynamic (Estes and Duggins 1995; Cohn 1998). The current Prince William Sound population is listed as stable or increasing under the Endangered Species Act, with close to 12,000 otters (Finerty et al., 2009; Estes and Duggins 1995; Cohn 1998; USFWS 2003).

1.8 Overall Research Objectives

The first objective of this study was to determine how the behavior of female sea otters changed as a function of pup development over time. In addition, the behavioral changes of the pup were also analyzed as a function of development (Chapter II). The second objective was to determine the differences in energy allocation by the female and the pup as the behaviors that are critical for survival are developed (Chapter III). The third objective was to estimate the total energy consumption necessary for the female and the pup throughout pup dependency (Chapter III).

CHAPTER II

DEVELOPMENT OF AN ALTRICIAL MAMMAL AT SEA: I. ACTIVITY BUDGETS OF FEMALE SEA OTTERS AND THEIR PUPS IN SIMPSON BAY, ALASKA

2.1 Introduction

Parental care is essential for the early survival of most mammalian offspring (Clutton-Brock, 1991). However, this is especially true for neonatal sea otters (*Enhydra lutris*), which are the most altricial of marine mammals born at sea. Sea otter pups are incapable of swimming for the first four-six weeks of life unlike cetaceans (whales and dolphins) and sirenians (manatees and dugongs) that can swim immediately after birth (Hanson et al., 1993; Kenyon, 1969; Osterrieder and Davis, 2011; Payne and Jameson, 1984). As a result, female sea otters must not only feed their pups, but also protect them from drowning, hypothermia and predation while at sea. Female mammals generally spend 80% of their reproductive lifespan caring for young (Gittleman, 1994), while male parental care occurs in fewer than 5% of all mammalian species (Clutton-Brock, 1991). Female sea otters provide continuous care, with no assistance from the male, until the pup is weaned at about six months of age, and this incurs a cost (i.e., increased foraging, reduced body condition, increased vulnerability to predation) in terms of her survival and the ability to successfully rear future offspring (Monson et al., 2000; Trivers, 1974; Zeveloff and Boyce, 1980).

Most of the mortality of dependent sea otter pups occurs during the first 60 days after birth with an average survival rate of 60% during the first three months (Monnett and Rotterman, 2000; Riedman et al., 1994; Siniff and Ralls, 1991). Factors that affect pup mortality are unclear, but probably include maternal condition, maternal age and/or experience, quality of maternal care, local variation in food supply and/or pollutants, the behavior and density of resident males and weather (Monnett and Rotterman, 2000). Among mammals, the amount of time and energy that a parent invests differs depending on whether the offspring are altricial or precocial. Altricial offspring are helpless and require postnatal care for an extended period of time as the young develop the skills necessary for survival (Künkele and Trillmich, 1997; Langer, 2008). Most mammals, including sea otters, produce altricial neonates (Derrickson, 1992).

Other otter species, such as European otters (*Lutra lutra*), river otters (*Lutra canadensis*) and the chungungo (*Lontra felina*), also have altricial pups, but they are born in a burrow (holt) on land rather than at sea (Estes, 1986; Gorman et al., 2006; Reed-Smith, 2012; Valqui, 2012). These pups rely on parental provisioning until around nine months for river otters (Shannon, 1998), while European otters are not self-sufficient until even later (13 months) (Carss, 1995).

In contrast, most marine mammals and ungulates are precocial and have well developed locomotor and sensory abilities (Derrickson, 1992; Hennemann, 1984). The young are born with a rapid development of inter-individual recognition between the female and the young, which is especially true in gregarious species (Nowak et al., 2000). Female mammals with precocial young may have an advantage by producing

larger offspring that are self-feeding. In species that have easily captured prey, precocial young are capable of hunting with the female (Case, 1978a). The precocial newborn giraffe calves can stand up and run an hour after birth and browse on leaves by the age of 3-4 weeks (Pellow, 1984; Bercovitch et al., 2004). However, dichotomous labeling of the development of neonates is misleading. Instead, it is more realistic to consider offspring development as a continuum (Zeveloff and Boyce, 1980). For example, young may be labeled as an intermediate type whose sensory systems are functional but thermoregulatory capabilities are inefficient, such as pigs, or locomotory capabilities are limited (primates) (Nowak et al., 2000).

Until sea otter pups are weaned and can survive on their own, there are four major causes of pup mortality that female sea otters must prevent or avoid: drowning, hypothermia, starvation and predation. Many of the behaviors exhibited by females during the early life of their pups are a response to these threats. Unlike most marine mammals that have a blubber layer for insulation in water, sea otters rely on fur for thermal insulation and an elevated resting metabolic rate to maintain a stable core body temperature of ca. 37^{o} typical of most mammals (Costa, 1982; Costa and Kooyman, 1982; Kenyon, 1969; Willams et al., 1992; Yeates et al., 2007). Grooming the fur is essential for maintaining an air layer adjacent to the skin, which provides 70% of the thermal insulation (Costa and Kooyman, 1982; Davis et al., 1988; Kenyon, 1969; Williams et al., 1992). Despite the critical importance of grooming for thermoregulation, young sea otter pups cannot groom themselves effectively and must rely on the female to groom them during the initial 8-10 weeks after birth (Payne and Jameson, 1984). The

combined inabilities of neonatal sea otters to swim and groom, two critical behaviors essential for survival, make them especially vulnerable to drowning and hypothermia and require the female's attention and care until these skills are perfected.

During gestation, the offspring of eutherian marine mammals (there are no metatherian marine mammals) derive all their energy from the female through the placenta, and provisioning continues postpartum during lactation as the energy requirements of the maturing neonate rapidly increase. Weaning marks the final transition from milk to solid food, and it may be abrupt or last months to years (Langer, 2008). In species such as sea otters, the female provides both milk and solid food for the physiologically immature (in terms of diving and foraging ability) and inexperienced young. Hence, the female must forage both for herself and her young until the pup is self-supporting. With an already elevated metabolic rate (resting metabolic rate is 2-3-fold greater than terrestrial mammals of similar size (Costa, 1982; Costa and Kooyman, 1982; Kenyon, 1969; Willams, 1989), the mass specific energetic demand on females is higher than most other mammals, especially just prior to weaning as pups approach a body mass and energy requirement similar to adults (Langer, 2008; Thometz et al., 2014). The female cannot sustain this heavy energetic demand for long periods and must balance the investment in a single offspring to maximize her lifetime reproductive success (Reid, 1995).

The activity budgets of lactating female sea otters indicate critical behaviors for successfully rearing pups, whereas the activity budgets of pups indicate the development and acquisition of behaviors and skills critical for survival that are acquired at different

stages of maturation up to the time of weaning (Hanson et al., 1993; Monnett and Rotterman, 2000; Payne and Jameson, 1984). Although the general behavior of lactating females and young pups has been described (Hanson et al., 1993; Payne and Jameson, 1984; Osterrieder and Davis, 2011; Thometz et al., 2014), the simultaneous behavior and activity budgets of wild female sea otters and their pups during early maturation have not been thoroughly quantified using direct observation even though they have a critical influence on individual fitness.

Behavioral observations of marine mammals at sea are difficult due to limited accessibility, sea state, natural light levels or the inability to observe them once they submerge (Schofield et al., 2006). For sea otters, some researchers have used abdominally implanted archival recorders and radio transmitters to track animals at sea and record the depth and duration of dives. These devices indicate when the animals are active or inactive, but cannot distinguish the full range of normal behaviors. In contrast, direct observations, when feasible, enable detailed descriptions of behavior and daily activity patterns, which are generally not possible with telemetry (Schofield et al., 2006).

In this study, we observed the behavior of female sea otters and their pups in Alaska. Our null hypothesis was that female behavior and activity patterns did not change as neonatal pups matured. To test this hypothesis, we used direct observation to determine the simultaneous 24-h activity budgets for females and their pups during the first three months postpartum, which represents the first half of the period of pup dependency and the time of greatest mortality (Monnett and Rotterman, 2000). Our

results provided new insight into pup maturation and their care and provisioning by the females during the early stages of pup development.

2.2 Materials and Methods

2.2.1 Study Site

Simpson Bay (ca. 60.6^{o} N, 145.9^{o} W) (Figure 2-1), was the preferred study site due to its protection from rough seas, reliable presence of sea otters and easy access. It was located in northeastern Prince William Sound and is ca. 21 km^{2} in area; 7.5 km long in the northern and western bays, 5 km long in the eastern bay and 2.5 km wide at the entrance of the bay (Wolt et al., 2012).

The average water depth in Simpson Bay was 30 m (maximum depth of 125 m) with a benthos primarily consisting of soft sediments (mud, mixed mud and gravel) and some rocky reefs (Gilkinson, 2011; Noll et al., 2009; Wolt et al., 2012). None of the large-bodied canopy-forming kelps (e.g., *Nereocystis*) are present, but large fronds of sugar (*Laminaria saccharina*), split (*Laminaria bongardiana*), and sieve (*Agarum clathratum*) kelp cover the benthos in many areas of the bay from the subtidal to a depth of approximately 10 m (RW Davis unpublished data). Male sea otters re-colonized Simpson Bay in 1977, while females subsequently moved into the area between 1983-85 (Garshelis, 1983; Rotterman and Jackson, 1988; VanBlaricom, 1988; Wolt et al., 2012). Since 2002, it has been used during the summer (June-August) by an average of 125 $\pm$ 15.2 sea otters, including adults and subadults (93 $\pm$ 9.0) and pups (32 $\pm$ 7.0) with an average summer density of 6.0 otters km^{-2} (updated from Wolt et al., 2012). During the

winter, the number of otters in the bay decreases to ca. 50, although where they disperse is poorly understood (Wolt et al., 2012). This research was conducted under a Letter of Confirmation No. MA-043219 from the U.S. Fish and Wildlife Service.

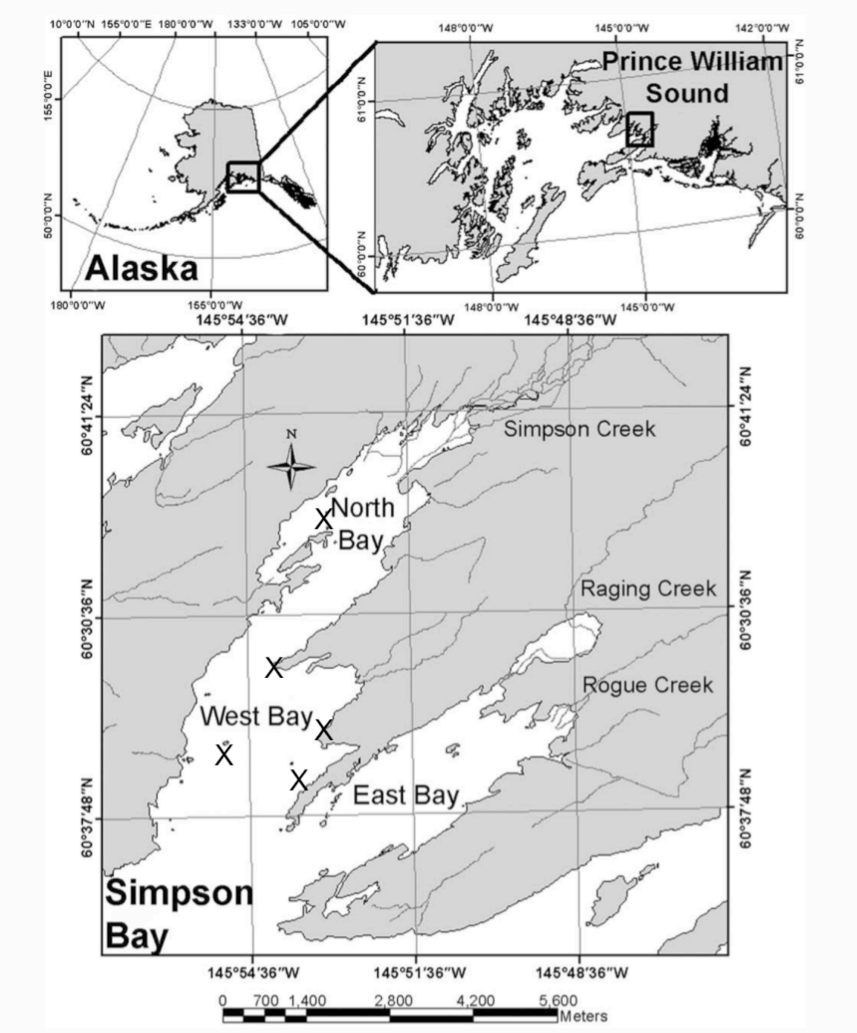

Figure 2-1. Simpson Bay, Prince William Sound, Alaska (reprinted with permission from Wolt et al., 2012). X's denote shore-based observation stations.

2.2.2 Boat-based Observations

The behavior of female sea otters with dependent pups was recorded from May to August of 2008-11. The high latitude of the study site made visual observations possible 24-h which were divided into four, 6-h time periods corresponding with astronomical dawn (05:00–11:00), day (11:00–17:00), dusk (17:00–23:00) and night (23:00–05:00). The research team, composed of a driver, recorder and spotter, made observations from a 7-m skiff. To maximize otter encounters, no systematic vessel track was followed. Instead, the skiff approached animals opportunistically on search paths that minimized the possibility of encountering an otter more than once during a 3–4 h session. However, the females were not tagged, so we could not be certain whether they were observed on subsequent days. When a female and pup were sighted, the skiff was maneuvered close enough (ca. 100 m) to observe their behavior with the aid of binoculars (Nikon 10-22x) without disturbing them. The behaviors of the female and pup were recorded simultaneously once per minute for 30 min (i.e., instantaneous focal follow; Altmann, 1974) before moving to another female and pup. If a female was disturbed, the observation was terminated and not included in the analysis.

The pups were divided into three behavioral and size classes (Categories 1-3) based on relative size, swimming ability and fur (i.e., lanugo, molting, adult pelage) (Table 2-1; Figure 2-2; Osterrieder and Davis, 2009; Payne and Jamseon, 1984). Category 1 pups (C1; ca. 0-<4 wks in age) were incapable of swimming or grooming and had a dense natal fur (i.e., lanugo). Category 2 pups (C2; ca. 4-<8 wk in age) exhibited coordinated swimming (but no diving or complex grooming behavior), had

begun to molt their lanugo, and were about half the female's body length. Category 3 pups (C3; ca. 8-12 wk in age) exhibited coordinated swimming and grooming, made short, shallow dives, had molted into their adult pelage, and were almost the same size as the female. The term C1, C2 or C3 female refers to a female with a C1, C2 or C3 pup, respectively.

Table 2-1. Behavioral and size class characteristics for pup categories (Adapted from Osterrieder and Davis, 2011).

	Age Estimate (Weeks)	Behavior	Length (compared to female)	Fur
Category 1	0 - <4	No swimming or diving	<50%	Dense natal fur
Category 2	4 - <8	Swimming with coordinated body movements; No diving	50-67%	Begins molting natal fur
Category 3	8 - 12	Swims and makes shallow dives[a]	68-75%	Molt complete with adult pelage

a: Dives longer than 30 sec.

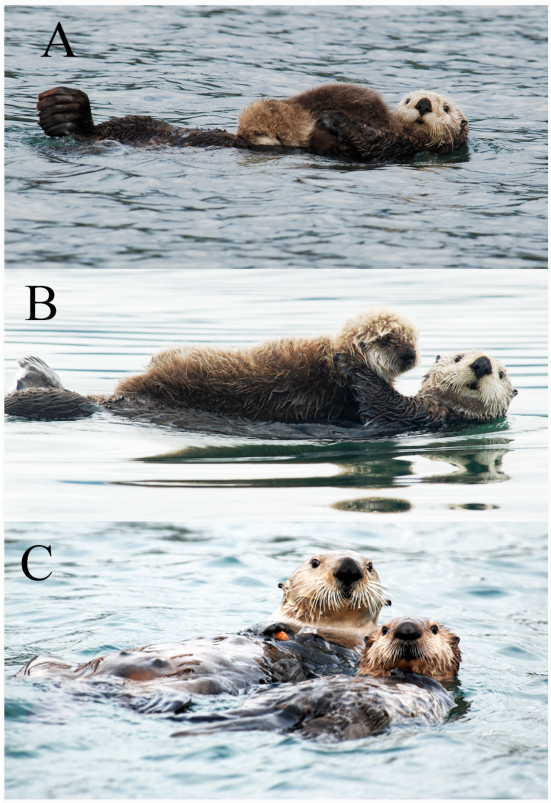

Figure 2-2. Pup Categories: (A) Category 1; (B) Category 2; (C) Category 3.

Six behaviors were recorded for the female (resting, swimming, feeding, pup-grooming, self-grooming, interacting), and seven behaviors were recorded for the pup (resting, swimming, feeding, nursing, self-grooming, being groomed, interacting) (Table 2-2). In this study, the term swimming for the female and older pups generally meant the animal was floating supine (on its back) at the surface using alternate pelvic paddling. Swimming for the C2 pups generally meant swimming prone (belly down), which differs from subsurface swimming during foraging when simultaneous pelvic paddling is used (Fish, 1996). For pups, the term feeding generally meant eating prey that was provided by the female, but included limited foraging for shallow prey items by C3 pups. Nursing was not recorded for the females as it occurred while the female was resting, swimming or pup grooming. Being groomed was used when the female groomed a pup that was not nursing. Time, tidal state, weather, water depth, and GPS location were also recorded for each focal follow.

Table 2-2. Female and pup behavioral state definitions.

Activity	Female	Pup
Foraging for the female, feeding for the pup	Foraging dives to the benthos using simultaneous pelvic paddling to acquire food, handling/ingesting prey; includes dives and interdive intervals	Handling/ingesting captured prey or begging/stealing prey from the female
Nursing	Only recorded for pup	Pup suckling while laying on the female's abdomen or along side
Self-Grooming	Vigorous rubbing, licking, aerating own fur	Vigorous rubbing, licking, aerating own fur
Being Groomed	Only recorded for pup	Female vigorously rubbing, licking and aerating the pup's fur
Pup-Grooming	Mother vigorously rubbing, licking and aerating the pup's fur	Only recorded for female
Interacting	Interacting with any otter including the pup; Can be social or reproductive	Interacting with any otter including the female and other pups
Swimming	Generally occurs at the surface, floating belly up and using alternate pelvic paddling but sometimes submerged using simultaneous pelvic paddling	Generally occurs at the surface, paddling belly down; Older pups begin using alternate pelvic paddling; Occasionally submerged swimming using simultaneous pelvic paddling
Resting	Floating belly up motionless or with slight movement of forepaws, head or feet; hauled out; sleeping	Laying on females' abdomen; floating belly up motionless or with slight movement of forepaws, head or feet; hauled out; sleeping

2.2.3 Shore-Based Observations

Because of the dense forest that surrounds Simpson Bay, shore-based observations of sea otter behavior are very difficult. In contrast, this is the preferred method for sea otter behavioral research in other areas (e.g., California) because of the high-energy (i.e., large ocean swell) coastline that makes boat-based observations logistically difficult and access to higher open vantage points (Estes et al., 1982; Estes et al., 1986; Ralls and Siniff, 1990). To compare results for these two observational methods, we also recorded the behavior of females and their pups from observations made at five shore locations (Figure 2-1) from May to August in 2010-11. These observations were performed during dawn (05:00–11:00), day (11:00–17:00) and dusk (17:00–23:00). Because higher light levels are needed for observing from shore through a telescope, no observations were performed at night.

The research team, composed of a spotter and recorder, made observations from alternating shore-based stations. Females and pups were observed opportunistically using a 50 – 80x telescope (Questar Corp., New Hope, Pa.). The behaviors of the female and pup were recorded simultaneously once per minute for four hours (i.e., instantaneous focal follow; Altmann, 1974) in a manner similar to the boat-based observations. Time, tidal state, weather, water depth, and GPS location were also recorded for each focal follow. If visual contact with a female was lost during the four-hour period, the observations were not used in the analysis.

2.2.4 Data Analyses

The percentage of time spent in each behavior recorded from boat-based observations was summed for each 6-h time period and for 24-h to make activity budgets for females and pups. The percentage of time spent in each behavior recorded from shore-based observations was also summed separately to compile a dawn to dusk activity budget. Multivariate analysis of covariance (MANCOVA) was used to test for correlations between female and pup behavior (the dependent variables) due to time of day and pup category (the independent variable) with year as a covariate to remove the influence of year if it was found to be significant using SPSS (Version 15 statistical software, Chicago, IL) at $\alpha = 0.05$. The mean time spent among the female and pup's behaviors for each category was tested using Tukey HSD post hoc tests.

A MANCOVA was also used to test for differences between the boat and shore-based methods among dawn, day and dusk activity budgets also with year as a covariate to remove the influence of year if it was found to be significant. However due to a smaller sample size (fewer observations in only three time periods), category was excluded from the analysis to reduce the number of dependent variables, so the boat-based observations from all categories (C1 to C3) were combined for this analysis. The shore-based observations were also subdivided into thirty minute samples for analysis.

2.3 Results

2.3.1 Boat-based Observations

In total, the behavior of 685 female-pup pairs (30 min periods) was recorded totaling 20,550 min. The percentages of observation time were similar (25-27%) among dawn, day and dusk, but slightly lower (21%) at night (Table 2-3). There were similar percentages of observation time for C1 and C3 pups (24% and 28%, respectively), but nearly twice as much (48%) for C2 pups. Sea otter pup births peak in the late spring and summer. We arrived in early summer after the initial developmental period of C1 pups and had to wait for the second peak in pup births for additional C1 pup observations. Our field season also ended before pups born later than mid-summer could reach the C3 category. Therefore, the pups were predominantly C2, which explains the distribution of the three categories.

Table 2-3. Total females with pups observed from June-August of 2008-2011 in Simpson Bay, Alaska subdivided into 6-h time periods and pup categories.

Pup		Diel Period			
Category	Dawn	Day	Dusk	Night	Total
1	33	52	44	38	167
2	83	78	87	78	324
3	57	55	54	26	192
Total	173	185	185	142	685

2.3.1.1 Females

A one-way MANCOVA revealed a significant multivariate main effect for pup category (Wilks' $\lambda = 0.645$, F (26, 1316) = 12.384, $p < 0.0001$). Over a 24-h period, the percentages of time devoted to swimming (F (2,671) = 12.986, $P < 0.0001$), feeding (F (2,671) = 24.894, $P < 0.0001$), pup grooming (F(2,671) = 15.851, $P < 0.0001$) and interacting (F(2,671) = 28.749, $P < 0.0001$) were all significantly different among females with different category pups (Table 2-4). Females with C1 pups spent most of the day resting (50%), swimming (21%) and grooming their pup (13%). Remarkably, the percentage of time devoted to feeding was only 9% and only 6% of the day was spent self-grooming (Figure 2-3). Females with C2 pups also spent most of the day resting (52%), swimming (16%) and grooming their pups (10%). However, the percentage of time spent feeding increased to 13%, and the remainder of the day was spent self-grooming (7%) and interacting (1%). In contrast, females with C3 pups spent less time resting (46%), swimming (8%) and grooming their pup (4%), whereas the percentage of time spent feeding increased to 32% with the remainder of the day spent self-grooming (5%) and interacting with other otters (5%). The C1 and C2 females groomed their pups significantly more and foraged less than the C3 females. C1 and C2 females also interacted significantly less with other otters than the C3 females.

Table 2-4. Activity budgets for female sea otters with different pup categories in Simpson Bay, Alaska.

	Percentage of Day		
Behavior	Category 1	Category 2	Category 3
Resting[a]	50 [b]	52 [b]	46 [b]
Swimming *	21 [b]	16 [c]	8 [d]
Feeding *	9 [b]	13 [b]	32 [c]
Pup Grooming *	13 [b]	10 [b]	4 [c]
Self-Grooming	6 [b]	7 [b]	5 [b]
Interacting *	0 [b]	1 [b]	5 [c]

Each asterisk indicates a significant difference at the $\alpha = 0.05$ level.
[a] Standard Deviations: Resting: 0.376; Swimming: 0.21; Feeding: 0.331; Pup Grooming: 0.149; Self-Grooming: 0.112; Interacting: 0.062
[b, c, d] Categories with differing letters were statistically significant ($\alpha = 0.05$) for each behavior

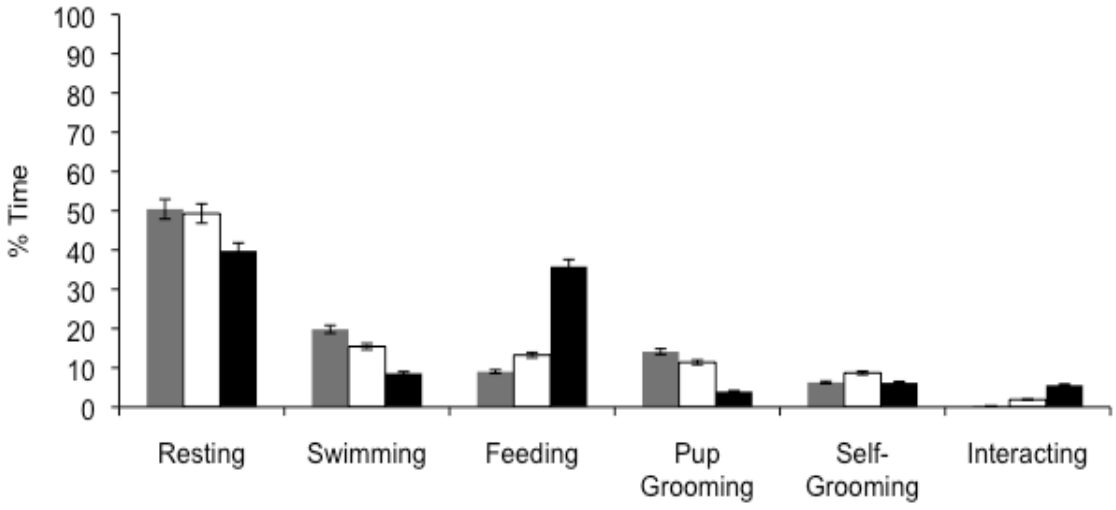

Figure 2-3. Comparison of female 24-h activity budgets in Simpson Bay, Alaska from 2008-2011 subdivided by pup category. Gray: Category 1; White: Category 2; Black: Category 3. The error bars represent 0.05% error.

Females with C1, C2 and C3 pups engaged in all six behaviors to varying degrees during the four, 6-h periods (Figure 2-4). During an average 24-h period for C1 females, most of the time spent was spent resting (12.3 h), which occurred more during dawn (31%), with similar amounts of time resting during the day, dusk and night (22-24%) (Figure 2-4A). The small amount of time spent feeding (2.0 h) occurred primarily during the day, dusk and night (85%). Swimming was the second most common behavior (4.9 h) and occurred primarily during day, dusk and night (92%), while self-grooming (1.6 h) occurred primarily during dawn (37%). Pup grooming (3.1 h) occurred primarily during the dawn and dusk (59%).

For C2 females, the amount of time spent resting (12.6 h) remained high and continued to occur predominantly during dawn, dusk and night (79%). The amount of time spent feeding increased 1.6-fold (3.2 h) and now occurred during dawn, day and dusk (78%) (Figure 2-4B). Swimming decreased (3.8 h) and occurred primarily during day, dusk and night (86%), while self-grooming increased (1.7 h) and occurred primarily during dawn, day and dusk (81%). Pup grooming also decreased (2.5 h) and occurred more during the day and dusk (56%) and nearly equal frequency during dawn and night (43%), while interacting increased slightly (0.3 h) and was concentrated during dawn, day and night (84%).

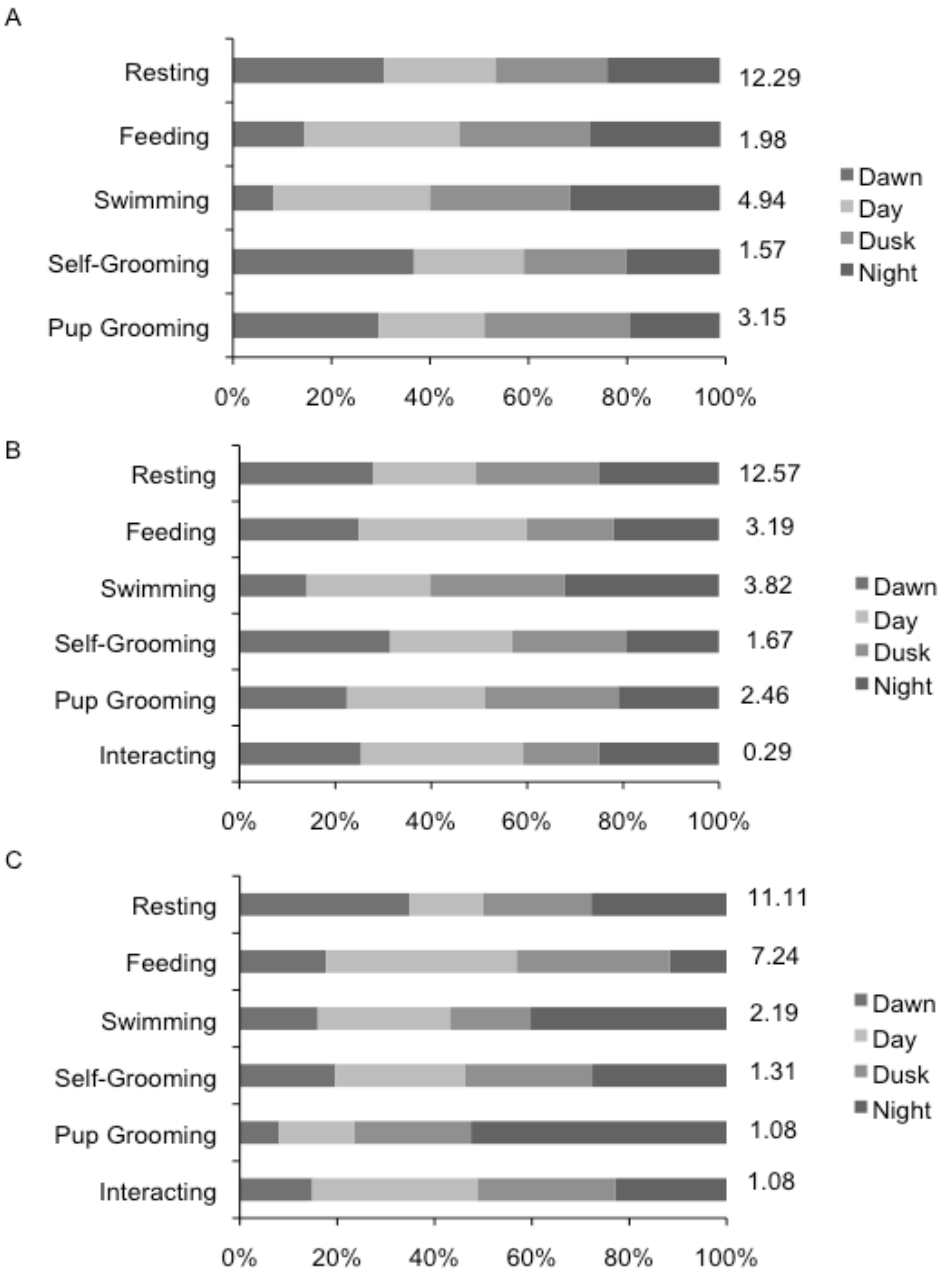

Figure 2-4. Female behavior as a function of time period: (A) Category 1 Female; (B) Category 2 Female; (C) Category 3 Female. The number of hours spent in each behavior is shown at the end of each bar.

For C3 females, the amount of time spent resting remained high, but decreased (11.1 h), and continued to occur during dawn, dusk and night (85%) (Figure 2-4C). The amount of time spent feeding increased 2.3-fold (7.2 h) and was now heavily concentrated during the day (40%) with the remainder primarily during dawn and dusk (49%). Swimming continued to decrease (2.2 h) and occurred primarily during day and night (67%), while self-grooming was little changed (1.3 h) and occurred equally throughout the 6-h time periods (~25%). Pup grooming continued to decrease (1.1 h) and occurred primarily during dusk and night (76%), while interacting increased 3.7-fold (1.1 h) and was concentrated during the day (33%) with the remainder primarily during dusk and night (51%).

2.3.1.2 Pups

Over a 24-h period, the percentage of time resting ($F(2,671) = 52.035$, $P < 0.0001$), feeding ($F(2,671) = 51.420$, $P < 0.0001$), swimming ($F(2, 671) = 29.284$, $P < 0.0001$), self-grooming ($F(2,671) = 9.538$, $P < 0.0001$), being groomed ($F(2,671) = 14.220$, $P < 0.0001$) and interacting ($F(2,671) = 21.742$, $P < 0.0001$) were all significantly different among categories (Table 2-5). C1 pups spent most of the day resting (83%) and the remainder being groomed (9%), nursing (7%) and attempting to swim (<1%) Figure 2-5) C2 pups also spent most of the 24-h period resting (73%), being groomed (7%) and nursing (8%). However, these pups spent part of the 24-h period in new behaviors, such as swimming (7%), attempted self-grooming (2%) and feeding on solid food provided by the female (2%). C2 pups also began to interact with other otters including the female

(2%). C3 pups spent only 48% of the 24-h period resting, which was comparable to the female. The percentage of time feeding on solid food (17%) and time swimming (17%) increased. The amount of time spent nursing (7%) was similar to the other pups but being groomed (2%) was much less. The self-grooming behavior (3%) was still being perfected.

Table 2-5. Activity budgets for different pup categories in Simpson Bay, Alaska.

	Percentage of 24-h Period		
Behavior	Category 1	Category 2	Category 3
Resting[a] *	83 [b]	73 [b]	48 [c]
Swimming *	0 [b]	7 [b]	17 [c]
Feeding *	0 [b]	2 [b]	17 [c]
Nursing	7 [b]	8 [b]	7 [b]
Self-Grooming *	0 [b]	2 [b]	3 [c]
Being Groomed *	9 [b]	7 [b]	2 [c]
Interacting *	0 [b]	2 [b]	6 [c]

Each asterisk indicates a significant difference at the $\alpha = 0.05$ level.
[a] Standard Deviations: Resting: 0.336; Swimming: 0.199; Feeding: 0.195; Nursing: 0.129; Self-Grooming: 0.047; Being Groomed: 0.126; Interacting: 0.083.
[b, c] Categories with differing letters were statistically significant ($\alpha = 0.05$) for each behavior

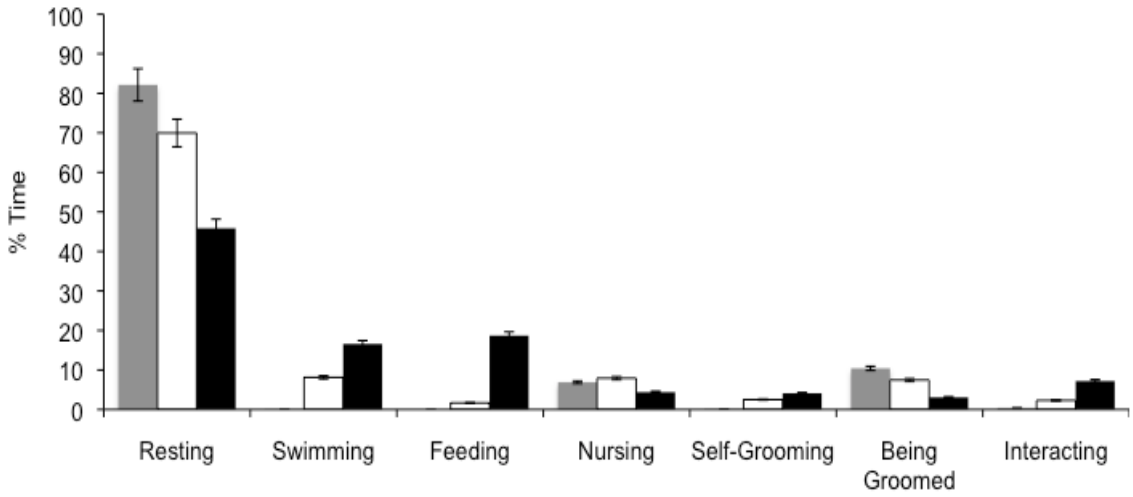

Figure 2-5. Comparison of pup 24-h activity budgets in Simpson Bay, Alaska subdivided into categories. Gray: Category 1 Pup; White: Category 2 Pup; Black: Category 3 Pup. The error bars represent 0.05% error.

C1 pups did not eat solid food and spent little or no time swimming, self-grooming and interacting, whereas C2 and C3 pups engaged in all seven behaviors to varying degrees during the four, 6-h periods (Figure 2-6). During an average 24-h period for C1 pups, resting predominated (19.7 h) and occurred with nearly equal frequency (23-26%) during the four, 6-h time periods (Figure 2-6A). Nursing (1.8 h) occurred primarily during dusk and night (58%) and being groomed (2.2 h) during dawn and dusk (66%).

For C2 pups, resting still predominated (17.5 h) and occurred with nearly equal frequency (23-26%) during the four, 6-h time periods (Figure 2-6B). Nursing (2.0 h) occurred more during dusk (31%) and in equal proportion during the dawn, day, and night (~23%) Swimming increased from <1% to 7% (1.7 h) and occurred mainly during the dawn, day and night (83%). Being groomed decreased (1.7 h) and occurred with

nearly equal frequency (22-29%) during the four, 6-h time periods. C2 pups began feeding on solid food provided by the female (0.4 h), which occurred primarily during the day (60%). This was similar to self-grooming (0.4 h), which occurred primarily during dawn, day and night (88%), and interacting (0.4 h), which occurred primarily during dawn and day (69%).

For C3 pups, resting decreased but still predominated (11.9 h) and occurred primarily during dawn, dusk and night (84%) (Figure 2-6C). Nursing (1.7 h) also decreased and occurred primarily during dusk and night (59%), while swimming increased (3.9 h) and occurred primarily during dawn and day (63%). Feeding on solid food increased 9.6-fold (3.8 h) and occurred primarily during the day and dusk (77%) similar to the female. Self-grooming also increased 1.7-fold (0.7 h), which occurred primarily during the day and night (69%). Being groomed showed little change (0.7 h) and occurred primarily at dusk and night (76%), but interacting increased 3.4-fold (1.3 h) and occurred primarily during dawn, day and dusk (85%).

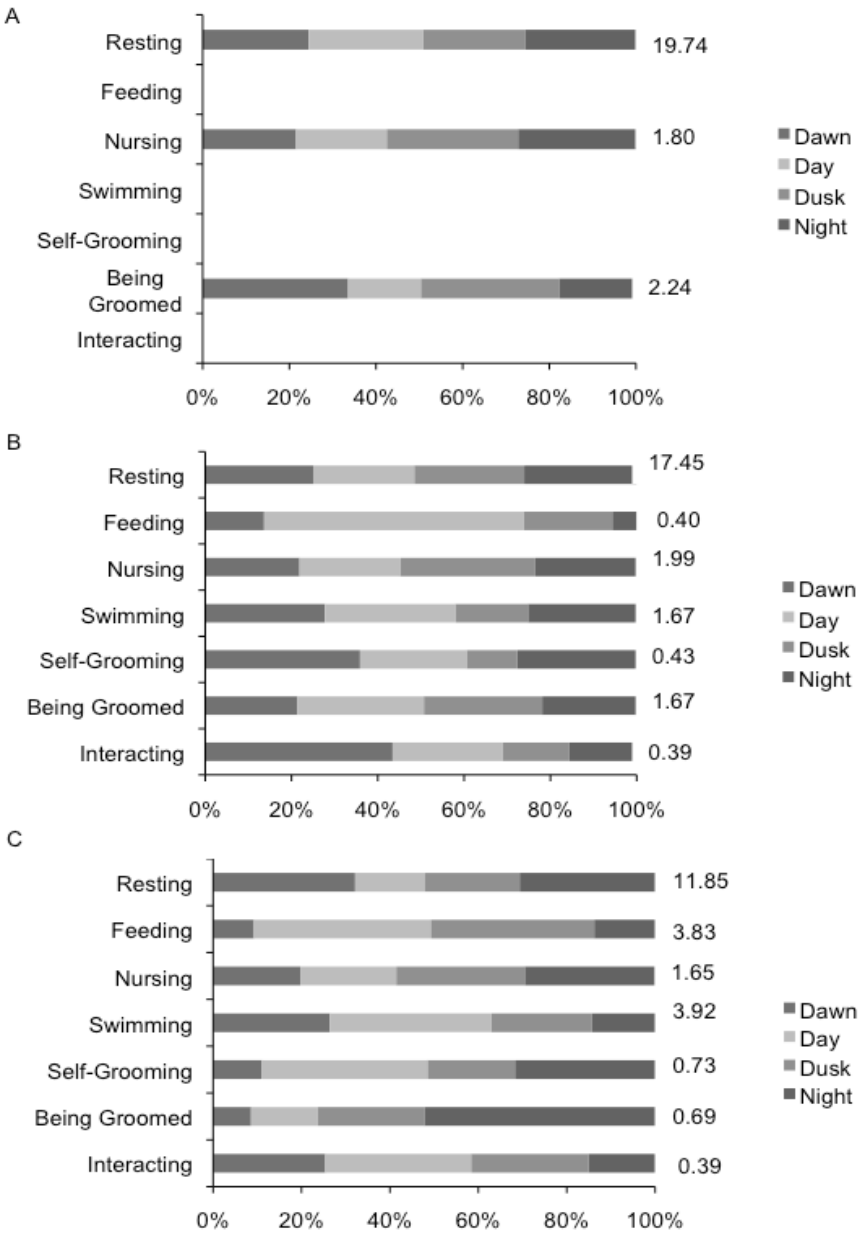

Figure 2-6. Pup behavior as a function of time period: (A) C1 Pup; (B) C2 Pup; (C) C3 Pup. The number of hours spent in each behavior is shown at the end of each bar

2.3.2 Shore-Based Observations

The behavior of 22 females with pups was recorded totaling 5,280 min using the shore-based method. There were no significant differences in the percentages of time that females spent feeding (F (1,713) = 0.008, P = 0.929) and interacting (F(1,713) = 0.368, P = 0.545) between the boat-based and shore-based methods (Table 2-6). There were small increases in the percentages of time that females spent swimming (14% to 20%) that were statistically significant (F (1,713) = 5.628, P = 0.018) and an equivalent amount of time self-grooming that was statistically significant (F (1,713) = 10.43, P = 0.002). Pup grooming increased slightly (9% to 12%) (F(1,713) = 6.321, P = 0.012) and resting also slightly decreased (50 to 42%) (F (1,713) = 6.664, P = 0.012) using the shore-based method as compared to the boat-based method.

There were no significant differences in the percentages of time that pups spent resting (F (1,713) = 1.048, P = 0.306), swimming (F (1,713) = 0..688, P = 0.407), feeding (F(1,713) = 0.533, P = .466), being groomed (F(1,713) = 2.374, P = 0.124), and interacting (F(1,713) = 1.369, P = 0.242) between the boat-based and shore-based methods (Table 2-7). There was a slight decrease in the time spent nursing (8% to 5%) (F (1,713) = 7.177, P = 0.0008) using the shore-based method and an increase in the amount of time the pup spent self-grooming (2% to 7%) (F (1,713) = 9.424, P = 0.002). Overall, none of the differences in female and pup activity budgets was indicative of behavioral disturbance associated with using the boat-based method.

Table 2-6. Comparison of female 24-h activity budgets for boat-based and shore-based methods.

	Percentage of Day	
Behavior	**Boat-Based Methods**	**Shore-Based Methods**
Resting	50	42*[a]
Swimming	14	20*
Feeding	19	19
Pup Grooming	9	12*
Self-Grooming	7	7*
Interacting	2	0

Each asterisk indicates a significant difference at the $\alpha = 0.05$ level.
[a] Standard Deviations: Resting: 0.368; Swimming: 0.313; Feeding: 0.339; Self-Grooming: 0.131; Pup Grooming: 0.172; Interacting: 0.013.

Table 2-7. Comparison of pup 24-h activity budgets for boat and shore-based methods.

	Percentage of Day	
Behavior	**Boat-Based Methods**	**Shore-Based Methods**
Resting	66	64 [a]
Swimming	9	9
Feeding	6	12
Nursing	8	5*
Self-Grooming	2	7*
Being Groomed	6	0
Interacting	3	2

Each asterisk indicates a significant difference at the $\alpha = 0.05$ level.
[a] Standard Deviations: Resting: 0.357; Swimming: 0.209; Feeding: 0.195; Nursing: 0.200; Self-Grooming: 0.083; Being Groomed: 0.119; Interacting: 0.021.

2.4 Discussion

2.4.1 Behaviors and Activities Critical for Pup Survival

After birth, the neonate must readjust to extrauterine life (e.g., breathing and nursing), which is crucial for survival (Jørgensen et al., 2001). The female cares for her young through this adjustment until weaning. Weaning periods in mammals vary dramatically from the 3-5 day lactation period in hooded seals (*Cystophora cristata*) to over 900 days in chimpannzees and orangutans (Hayssen, 1993). In our study area, the average duration of pup dependency is 5.7 months (Monnett and Rotterman, 2000). As pups mature and develop their own survival behaviors or abilities, the activity budgets of females also change. Hence, the behavior of the females and young pups are complementary (i.e., combining in such a way as to enhance pup survival) and constantly changing as pups mature towards weaning and independence.

2.4.1.1 Drowning

Despite all the adaptations that marine mammals exhibit for living at sea, they never reacquired the ability to breathe water and are therefore susceptible to drowning. Most pinniped pups are precocial at birth and have the advantage of being terrestrial (or on ice) after birth until weaning (Horning and Trillmich, 1997; Ellis et al., 2000). However, neonatal sea otters are born in the ocean and cannot swim making them highly susceptible to drowning. In captivity, observations of sea otter pups have demonstrated that newborns sink shortly after death (Sherrod et al., 1975). Adult sea otters are excellent swimmers that use alternate or simultaneous strokes of the hind-paws (alternate

and simultaneous pelvic paddling) for propulsion at the surface in a supine position and simultaneous strokes underwater or at the surface in a prone position (Fish, 1996; Williams, 1989). In addition, they also have a lung volume that is substantially larger than a terrestrial mammal of similar size, which makes them positively buoyant and enables them to rest and sleep effortlessly at the surface (Lenfant et al., 1970). As a result, the female carries the neonatal pup on her abdomen as she swims at the surface, in essence serving as a moving island in the ocean. The modified hind-paws (digits are elongated, webbed and the fifth digit is the longest) enable females to paddle at the surface while attending to the pup, an ability unique among marine mammals.

While the female is making feeding dives, she leaves the pup floating at the surface. The pup's lanugo (i.e., neonatal fur) traps a layer of air next to the skin and makes the pup positively buoyant so that it can rest effortlessly at the surface. In our study, C1 pups, which were incapable of swimming, were the most susceptible to drowning even with their lanugo, so the females spent most (91%) of their time at the surface caring for the pups and only 9% of their time making feeding dives. It takes about four weeks for the pup to develop the coordination and the muscular strength for surface swimming and several more weeks before it begins making short duration, shallow dives with the female (Kenyon, 1969; Payne and Jameson, 1984). More mature C2 and C3 pups developed coordination and muscular strength to perfect swimming, and this enabled females to spend less time carrying their pups and devote more time to other behaviors such as feeding.

2.4.1.2 Hypothermia

Water conducts heat 25-fold faster than air, which makes sea otters susceptible to hypothermia in the cool waters of the North Pacific. Sea otters rely on fur that traps an air layer next to the skin and provides 70% of the thermal insulation (Kenyon 1969; Costa and Kooyman 1982; Davis et al., 1988; Williams et al., 1992). In contrast, most marine mammals rely on blubber for thermal insulation, so grooming is not required. To maintain this air layer, sea otters felt and aerate their fur by grooming, a behavior that is critical for maintaining a stable core body temperature (Costa and Kooyman 1982; Williams et al., 1988; Davis et al., 1988). When a sea otter is born on the surface of the water, its fur is wet and provides little thermal insulation. Since neonatal sea otters are unable to groom their fur, the female grooms the pup to establish this thermal insulating air layer.

As with sea otter pups, Northern fur seal pups (*Callorhinus ursinus*) are born with a natal fur that allows water to penetrate to the skin thereby providing littler thermal insulation when wetted. However, they rarely enter the ocean and spend most of their time on land until they molt into their adult pelage which traps air next to the skin and enables them to thermoregulate in water (Donohue et al., 2000). Likewise, altricial neonatal polar bears also have a fine hair coat and no subcutaneous fat for thermoregulation in water until they molt into their adult pelage. which improves thermoregulation in air and water (Kenny and Bickel, 2005).

Female sea otters rarely leave their pups on land; so neonatal pups must have waterproof fur for thermal insulation at birth. As pups develop the gradual ability to self-

groom, pup grooming by the female decreased. Hence, the total time devoted to pup grooming (provided by the female and the pup) was 13% for C1 pups, 12% for C2 pups and 7% for C3 pups. The decrease in total time devoted to grooming in C3 pups coincided with the molt of their lanugo and its replacement with adult fur. It appears that neonatal lanugo, which is longer than adult fur, may require additional grooming for it to retain an insulating air layer, and this grooming requirement decreases to about 7% of the activity budget for adults and pups that have molted into their adult fur.

2.4.1.3 Starvation

Without a thick blubber layer as an energy reserve, sea otters must forage daily throughout the year and are susceptible to rapid starvation (i.e., loss of muscle mass as the body breaks down these tissues for energy) if feeding is interrupted (Costa and Kooyman, 1982; Davis et al., 1988). Since young pups cannot forage for themselves, they depend on the female for milk and, as they mature, on solid food provided by the female (Payne and Jameson, 1984). Starvation is the greatest cause of pup mortality in pinnipeds (Mattlin, 1978). Female phocid seals typically have a shorter period of pup dependency because they fast (or greatly reduce food intake) throughout lactation (Boness and Bowen, 1996). They rely on energy stored as blubber for milk production and to satisfy their own metabolic requirements. In contrast, female otariids fast for the first week postpartum, but then make repeated foraging trips to obtain sufficient energy for themselves and lactation costs (Bowen, 1991; Boness and Bowen, 1996). As the pups

grow, otariid females lengthen their foraging trips to obtain additional energy until the pups are finally weaned (Boness and Bowen, 1996).

Sea otter females are comparable to the otariid females, because they feed throughout the period of pup dependency. C1 pups obtained all of their nourishment from nursing, which occupied 7% of their daily activity budget. It is unclear how females with C1 pups were able to support both their own metabolic requirements and those of the pup when they spent only 9% of their time foraging during the first two weeks postpartum. Pregnant females may develop some subcutaneous fat in the dorsal caudal area (R.W. Davis unpublished data), mesenteric and renal fat around the small intestines and kidneys, respectively, or in the inguinal area (V.A. Gill unpublished data). This may allow females to reduce foraging without entering a state of starvation and devote more time to caring for their pup during the critical first two weeks when the neonate is very vulnerable to hypothermia and predation. However, additional research is needed to understand how the females balance their energy requirements and those of the pup during this period of complete neonatal dependency.

As the pups matured and their energy needs increased, females, similar to otariid females, increased foraging effort to feed themselves and their pups (Boness and Bowen, 1996). In foraging bouts with ten dives or greater, 17% of the prey captured by C2 females was shared with their pups, and this increased to 25% for C3 females (M Cortez unpublished data). Even with an increase in solid food provided by the female, the percentage of the time that the pups spent nursing remained constant at 7-8%. Milk yield in mammals rises until peak lactation is reached, after which there is a decline in yield

until weaning (Blaxter, 1989). Even with similar nursing percentages, the amount of milk consumed by C2 and C3 pups was probably greater due to their larger stomachs and their increase in efficiency at ingesting more milk (Blaxter, 1989). At peak lactation, the additional energy requirements of the growing pups come from the ingestion of solid food provided primarily by the female.

Before sea otter pups can forage on their own, they must acquire the coordination and strength to swim and the physiological development for breath-hold diving. When a female is foraging, she leaves the pup at the surface where is rests passively. C2 pups showed the first signs of coordinated surface swimming, which occurred primarily while the females were foraging. C2 pups began making short, shallow dives after 6-8 weeks, but air in their lanugo made this challenging due to its buoyancy and the short breath-hold capability of young pups (Kenyon, 1969; Payne and Jameson, 1984). At this stage, females provide prey to the pups, and they are often seen manipulating and eventually consuming these items. Since the C3 pups had molted into their adult pelage, they began to make shallow dives with the females, often while the female was foraging. Observational learning and practice by sea otter pups may be an important for acquiring foraging skills as it is in river otter pups (Carss, 1995; Mann, 2008).

As the C3 pups began to forage with the female, they captured about 33% of prey they consumed during short, shallow dives and usually surfaced with small clams (i.e., *Saxidomus gigantea*) (M Cortez unpublished data). Even though the percentage of time that sea otters spend foraging can be as high as 50% (Gelatt et al., 2002; Finerty et al., 2009; Thometz et al., 2014), the heavy energetic demand placed on the female by her

own elevated metabolic rate and that of the pup, especially as pups approach a body mass and energy requirement similar to adults, cannot be sustained indefinitely and is probably ameliorated as the pup begins to forage on its own.

2.4.1.4 Predation

Sea otters are susceptible to predation by killer whales and sharks (Estes et al., 1998; Kreuder et al., 2003). Bald eagles, which are common around Simpson Bay, are also known to prey on very young sea otter pups left alone on the surface while females forage (Sherrod et al., 1975; Anthony et al., 2008). In Amchitka, Alaska, females with pups less than three weeks of age decrease their foraging time from ca. 43% to 21% and forage more at night due to potential risk of bald eagle predation (Gelatt et al., 2002). C1 females in Simpson Bay spent about 21% of their time swimming around the study area carrying their pups, often making long, meandering loops that brought them back to the same location without any apparent reason. We can only speculate on the reason for this behavior, but it may be related to predator avoidance. By reducing the time that newborn pups are left unattended at the surface and by moving around the study area, females may be engaging in predator avoidance. Vigilance, which is the awareness by females for any threat to the survival of their offspring, has been documented in other marine mammals including bottlenose dolphins (Hill et al., 2008). Meandering swimming decreased for C2 and C3 females as the pups grew and the potential threat of bald eagle predation diminished.

2.4.2 Other Behaviors and Activities

2.4.2.1 Resting

In this study, adult females spent 46-52% of their time resting or sleeping. In contrast, C1 pups spent most of their time resting which decreased to 48% for C3 pups. Young mammals sleep for long periods, but their rest and sleep patterns gradually coincide with that of adults. Hence, resting is an important body maintenance behavior that occupies about 50% of the day for adult female sea otters and older pups.

2.4.2.2 Interacting

Interacting is a behavioral category that includes different types of social behavior. For adult females, it often means mating attempts by males. These interactions are short in duration and devoid of any copulatory behavior at the surface, which makes impregnation unlikely. For pups, this category includes female-neonate interactions and eventually interactions with other sea otters. Females with C1 pups completely avoided interactions with other otters, but females with more mature pups spent more time interacting with their pups and other otters. C1 pups were incapable of interactive behavior that we could discern. However, C2 and C3 pups were noticeably more social and interacted at the surface with other otters while the female was foraging (M. Cortez unpublished data). Females with C3 pups often allowed more separation between themselves and their pups than C1 females. The pup will often approach other rafts and disturb resting sea otters.

Play behavior is important in different species because it promotes physical conditioning, socialization, sensorimotor/cognitive skills and development of foraging skills (Bekoff, 1989; Carss, 1995). In addition, early play behavior may strengthen and maintain social bonds formed between the young and adults (Bekoff, 1989). Play behavior is commonly seen in other otter species. About 30% of the daily activity of the juvenile giant river otter (*Pteronura brasiliensis*) is associated with play and is even seen 7 to 12% of the time in the adult's activity budget as well (Londoño and Muñoz, 2006). In immature river otters, play accounted for 6% of their daily activity is associated with wrestling and chasing other river otters along with playing with prey (Melquist and Hornocker, 1983). It is also common among other marine mammal neonates, such as chasing, displaying and object carrying in dolphins (Mann and Smuts, 1999). In Galápagos fur seal pups, play behavior includes mock-fighting, chasing, exhaling in water, chewing on inanimate objects, and wiggling (Arnold and Trillmich, 1986). It is difficult to interpret the importance or significance of play behavior, but it is common to many young mammals including sea otter pups.

2.4.3 Differences Between Boat-based and Shore-based Activity Budgets

Simpson Bay is surrounded by a temperate rainforest with only a few vantage points for making shore-based observations of sea otters. In addition, this method is very light limited because of the greater distance between the observer and the otter. In this regard, boat-based observations have the advantage in being more flexible in locating and following otters and making observations under lower light conditions. However, the

question arises as to whether boat-based observations alter the behavior of sea otters, most probably as a function of the proximity between the boat and the animal.

In this study, we maintained a distance of at least 100 m while observing sea otters from a skiff. Since otters could be seen from a distance of many hundreds of meters, we could determine their behavior before we approached them in the skiff. Based on behavior before and after the skiff was positioned 100 m from the otter, we are convinced that this method does not alter the animal's behavior. We tested this assertion by conducting shore-based observations using methods and a telescope that were identical to those used in similar studies of sea otters in California (Estes et al., 1982; Estes et al., 1986; Ralls and Siniff, 1990) and found only minor differences that were statistically significant. The shore-based method recorded a small decrease in the percentages of time spent resting and interacting and a small increase in swimming and pup grooming (Table 2-6). If the skiff were affecting the otter's behavior (i.e., the otter was avoiding the skiff), we would expect the opposite result except for pup grooming. Likewise, there was little or no difference in the time budgets of pups using the two methods (Table 2-7). Furthermore, the boat-based method provided more detailed behavior observations and could be used under lower light levels that enabled 24-hr activity budgets.

Direct observations contribute important information for understanding the development of pup behavior that cannot be obtained by telemetry. Information about behavioral interactions between the pups and females or other otters is essential to understanding how the surrounding community is affected (Schofield et al., 2006).

Using these recorded observations, a wider range of behaviors can be analyzed (Schofield et al., 2006). Direct behavioral studies are essential for examining ontogenetic patterns and how the young survive early on or late in reproduction (Bekoff, 1989).

2.5 Conclusion

Many of the behaviours exhibited by females during the early life of their pups are a response to threats to survival. As pups mature and develop their own survival behaviours or abilities, the activity budget of females also changes. C1 pups, being the most susceptible to drowning, were only left unattended 9% of their time. Females also had to maintain the thermoregulatory properties of the pup's fur and spent 13% of the day grooming C1 pups. This declined in C2 and C3 pups as they began to develop the coordination to self-groom. Although pups with lanugo may require additional grooming, adult sea otters and pups that have molted into their adult fur groom about 7% of the day. The percentage of the time that all pups spent nursing remained constant at 7-8%. Although C1 pups obtained all of their nourishment from nursing, the additional energy requirement of older pups came from feeding on solid food provided primarily by the female.

Overall, there were only minor differences in recorded behaviour of females and pups between boat-based observations from a distance of 100 m and shore-based observations with a telescope. How females with C1 pups could support both their own metabolic requirements and those of the pup when they spent only 9% of their time foraging and why they spent 21% of their time meandering swimming are questions for

further consideration. Further research is also needed on the activity budgets of females and pups during the autumn and winter, which is the most energetically demanding time for females as pups approach weaning and weather conditions become much colder.

CHAPTER III

DEVELOPMENT OF AN ALTRICIAL MAMMAL AT SEA: II. ENERGY BUDGETS OF FEMALE SEA OTTERS AND THEIR PUPS IN SIMPSON BAY, ALASKA

3.1 Introduction

Mammalian female reproductive effort can be defined as the additional energy required for supporting offspring from the moment of pregnancy until weaning (Millar, 1977; Beck et al., 2003; Gittleman and Thomson, 1988). During pregnancy, energy and nutrients are provided to the fetus through the placenta (eutherian mammals), and the small, developing fetus obligates only a slight increase in female metabolism (Case, 1978a; Gittleman and Thompson, 1988). After birth, milk via female lactation provides energy for neonatal thermogenesis, activity and growth until the offspring is fully weaned.

For the female, lactation is the most energetically demanding phase of reproduction and the most susceptible to failure (Millar, 1977; Costa et al., 1986; Costa & Gentry, 1986; Jenness, 1986; Gittleman and Oftedal, 1987; Gittleman & Thompson, 1988; Boyd, 1998; Rogowitz, 1996; Gamel et al., 2005). Female mammals often face a choice of either allocating resources to existing or future offspring, and this choice will ultimately affect lifetime reproductive success and fitness (Parent-Offspring Conflict) (Gonzalez-Voyer and Kolm, 2010).). If resources are scarce, adults may abandon offspring to maintain body condition, so that they can breed again when conditions improve. If the young are nearly self-sufficient, abandonment is part of normal weaning

(Gonzalez-Voyer, 2010). However, very young mammals will starve if abandoned. Although all female mammals supply milk to their young, the duration of lactation varies across species (Case, 1978a; Balshine, 2012). Lactation length can be as little as 4 or 5 days in phocids or 2-3 months in domestic dogs (Pal, 2004; Lefèvre et al., 2010) However, lactation periods can last as long as 9-12 months in giraffes or even over 900 days in chimpanzees and orangutans (Pellow, 1984; Lefèvre et al., 2010). Even after weaning, the mother and young of some species, such as in primates, may remain together for years enabling offspring to learn foraging skills and predator avoidance tactics (Gijsbertus et al., 2006).

Neonatal growth from new tissue synthesis is greater than during any other stage of development (Davis et al., 2008) and requires energy, protein, calcium and other macronutrients (Speakman, 2008). There are many factors that influence growth rate, including precociality/altriciality, brain size, birth weight and feeding habits (Case, 1978b). Altriciality is characterized by rapid prenatal development throughout gestation, which is not as energetically costly as lactation, and provides the female with the option of sharing postnatal costs with a male or kin alleviating some of the increased energetic cost to the female (Case, 1978a). Altricial mammals are less developed at birth in regards to thermoregulation, activity and suckling efficiency and have slower postnatal growth rates compared to precocial mammals (Gaillard et al., 1997). Some pinnipeds, cetaceans, and canids have the highest growth rates and efficiencies, whereas other aquatic species and most other fissiped carnivores grow at more moderate rates. The fastest relative growth rates have been recorded in seals (Order Carnivora, Family

Phocidae), with young ribbon and harbor seal pups growing at rates 70-fold greater than human infants (Case, 1978b).

Once a female reaches peak milk production, further energy demands by the growing pup can no longer be provided by lactation alone. At this point, the young begin eating solid food to supplement milk to meet their daily energetic demands (Langer, 2008). This is beneficial to the female and initiates the weaning process, which may be gradual or abrupt (Langer, 2008). At full weaning, the young have achieved a degree of independence and are capable of foraging independently, although mortality is often high during the first year (Galef, 1981). The weaning mass of young mammals influences survival and serves as an indicator of total maternal effort and population stress (Lee, 1991; Boltnev et al., 1998).

The resting metabolism of adult sea otters is 2-3 times higher than that of similar-sized terrestrial mammals, and they must consume about 25% of their body mass in food each day (Kenyon, 1969; Yeates et al., 2007; Finerty et al., 2009; Osterreider and Davis, 2009). Young aquatic mammals have higher mass specific metabolic rate than adults, which is necessary to maintain a stable core body temperature of 37^{o} C in the marine environment (Thompson et al., 1987). As a result, the energetic demand on female sea otters to sustain their own metabolic requirements and those of their maturing pups is very high and ultimately may influence the time of weaning.

Lactation can result in a three-fold increase in resting energy metabolism relative to a non-breeding female (Costa et al., 1986; Gittleman and Thompson, 1988; Rogowitz, 1996). In most canids (Famile: Canidae), pairs or groups defend a territory and all adults

help defend and provide food for the young, while possibly even providing food for the female (Malcolm, 1985). However, most mammalian females raise young without the help of males or other adult helpers (Gittleman, 1994), and the females must incur this elevated cost of lactation independently. Females can compensate for an increase in energetic demand during lactation by mobilizing energy stores (mainly fat), increasing food consumption or reducing energetically expensive activities (Gittleman and Thompson, 1988; Rogowitz, 1996; Mellish et al., 2000; Bowen et al., 2001). The particular compensatory strategy used will have an impact on the growth and development of the offspring (Burns, 2004).

Female polar bears fast during the final phase of gestation and initial phase of lactation in the den and rely on body fat and protein for milk production. Depletion of female fat stores, if food is scarce, can result in cub starvation due to the cessation of lactation (Derocher and Stirling, 1998). Among marine mammals, seals and baleen whales (Order Cetacea, Suborder Mysticeti) will reduce activity and thermoregulatory costs (through migration to warmer waters) and rely on internal energy reserves (e.g., blubber) to support lactation until offspring are weaned (Gittleman and Thompson, 1988; Bonnet et al., 1998; Boyd, 1998; Beck et al., 2003; Skiebel et al., 2013). This strategy is referred to as capital breeding, in which feeding and reproduction are spatially and temporarily separated and include a fasting period during offspring development. Mammals that use a fasting compensatory strategy produce milk with low carbohydrate and high fat concentrations (Oftedal, 2000). For example, phocids usually rely on a rapid weaning strategy and supply their offspring with milk that has a high fat content (25-

60%) leading to rapid formation of adipose tissue in the young (Bonness and Bowen, 1996; Gamel et al., 2005). This lowers the metabolic overhead of the female allowing for a greater energy transfer to the offspring (Boyd, 1998).

The most common compensation method for increased energetic demands due to lactation is to increase food intake, which can be 1.7 to 2.9-fold greater than that of non-lactating females (Costa et al., 1986; Gittleman and Thompson, 1988; Rogowitz, 1996; Mellish et al., 2000). Many otariids exhibit an income-based foraging strategy, where they feed throughout a long lactation period and produce milk with a lower lipid (17-45%) and energy content (Costa et al., 1986; Bonness and Bowen, 1996; Burns, 2004; Gamel et al., 2005). This income-based compensatory strategy allows for the gradual formation of lean tissue rather than a blubber layer in pups (Burns, 2004; Gamel et al., 2005) and thus, reduces loss of body mass in the female (Skiebel et al., 2013).

The goal of our study was to construct simultaneous energy budgets for wild female sea otters and their pups during the first three months postpartum based on the detailed activity budgets for each (Cortez et al., in review) and published metabolic rates of certain behaviors in captive sea otters. These simultaneous energy budgets may demonstrate the heavy energetic demand placed on female sea otters as they care for the most altricial marine mammal neonate born at sea.

3.2 Materials and Methods

3.2.1 Study Site

Simpson Bay (ca. 60.6° N, 145.9° W) is a relatively shallow bay located in northeastern Prince William Sound, Alaska, with an average water depth of 30 m (maximum depth 125 m). It is approximately 21 km^2 in area - 7.5 km long in the northern and western bays, 5 km long in the eastern bay and 2.5 km wide at the entrance of the bay. Simpson Bay is a well-studied site for sea otter ecology (Gilksinson et al., 2007; Finerty et al., 2008; Osterrieder and Davis, 2009; Osterrieder and Davis, 2011; Wolt et al., 2012), because of its easy access, protection from rough seas, and reliable presence of sea otters (Figure 3-1).

The benthos consists primarily of soft sediments (mud, mixed mud and gravel) with some rocky reefs (Gilkinson, 2004; Noll et al., 2008). None of the large-bodied kelps (e.g., *Nereocystis*) that elsewhere form canopies are present, but large fronds of sugar (*Laminaria saccharina*), split (*Laminaria bongardiana*), and sieve (*Agarum clathratum*) kelp cover the benthos in many areas of the bay from the subtidal to a depth of approximately 10 m (R. W. Davis, pers. obs.). The bay was re-colonized by male sea otters in 1977, and females moved into the area between 1983-85 (Garshelis, 1983; Rotterman and Simon-Jackson, 1988; VanBlaricom, 1988). Since 2002, this Alaskan bay has been used during the summer (June-August) by an average of 125 $\pm$ 15.2 sea otters, including adults and subadults (93 $\pm$ 9.0) and pups (32 $\pm$ 7.0), giving an average summer density of 6.0 otters km^{-2} (updated from Wolt et al., 2012). During the winter, the number of otters in the bay decreases to ca. 50, although where they go is poorly

understood (Wolt et al., 2012). This research was conducted under a Letter of Confirmation No. MA-043219 from the U.S. Fish and Wildlife Service.

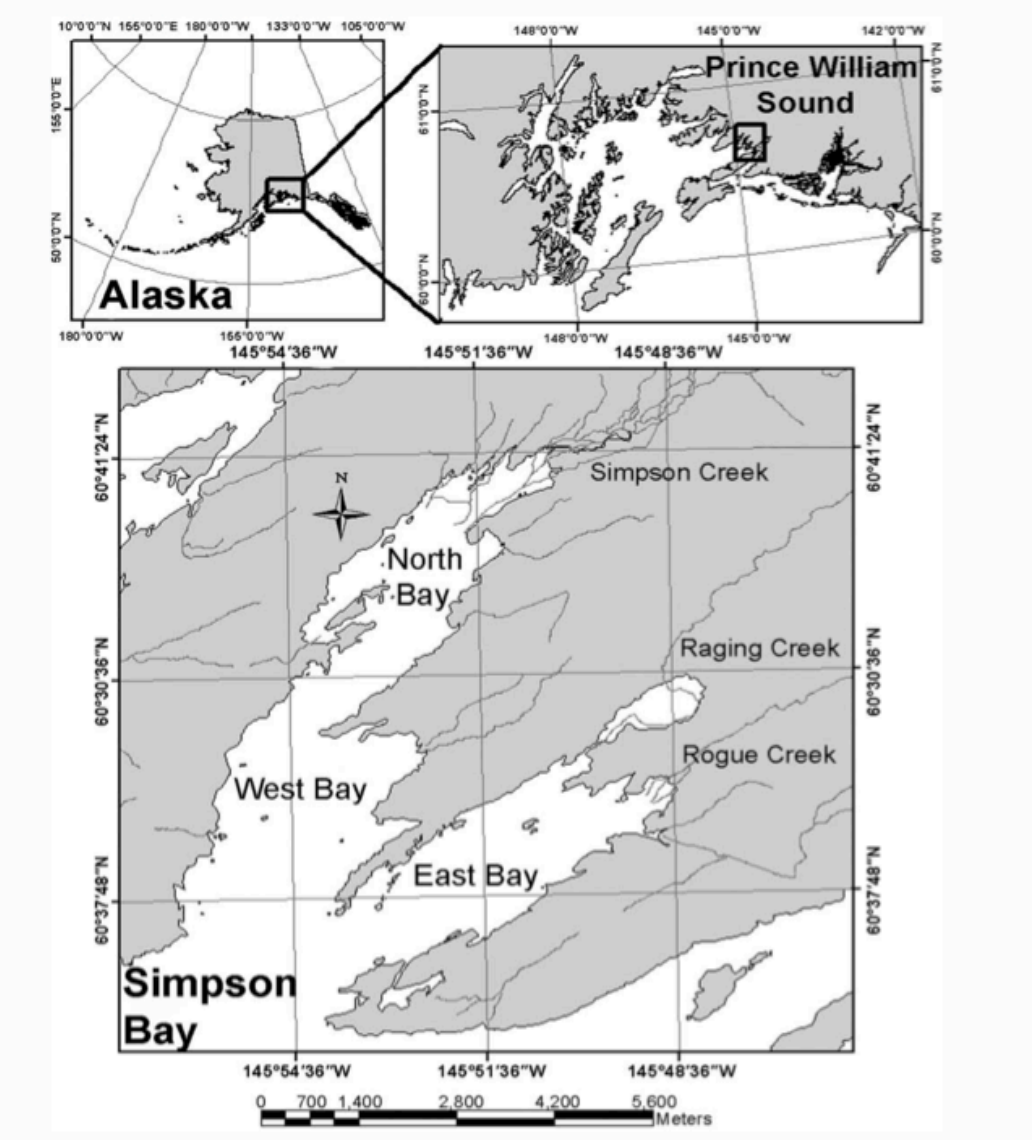

Figure 3-1. Simpson Bay, Prince William Sound, Alaska (reprinted with permission from Wolt et al., 2012).

3.2.2 Activity Budgets

Data collection for the activity budgets of females and pups has been described (Cortez et al., in review). Briefly, we recorded the behavior of female sea otters with dependent pups during the summer months of May-August 2008-11. The research team, composed of a driver, recorder and spotter, made observations from a 7-m skiff. When a female and pup were sighted, the skiff was maneuvered close enough (ca. 100 m) to observe their behavior with the aid of binoculars (Nikon 10-22x) without disturbing them. The behaviors of the females and pups were recorded simultaneously once per minute for 30 min (i.e., instantaneous focal follow; Altmann, 1974) before switching to another pair. On the rare occurrence that a female showed signs of disturbance (e.g., swimming away from the skiff), the behavioral observations were not included in the analysis.

Six behaviors were recorded for females (resting, swimming, feeding, self-grooming, pup-grooming and interacting) and seven behaviors were recorded for associated pups (resting, swimming, feeding, self-grooming, being groomed, nursing, interacting) (Appendix A-1). The pups were divided into three behavioral and size categories (Categories 1-3) based on relative size, swimming ability and fur (i.e., lanugo, molting, adult pelage) (Table 3-1). Category 1 pups (C1; ca. 0 - <4 wk in age) were incapable of swimming or grooming and had dense natal fur (i.e., lanugo). Category 2 pups (C2; ca. 4 - <8 wk in age) exhibited coordinated swimming abilities and were about half of the length of the female. Category 3 pups (C3; ca. 8 - 12 wk in age) were about the size of the females and molted into adult pelage. These pups had also developed their

swimming and diving abilities. The percentage of time spent in each recorded behavior was summed to compile 24-h female and pup activity budgets.

Table 3-1. Criteria for estimating the three age categories for pups (Adapted from Osterrieder and Davis, 2010).

	Age Estimate (Weeks)	Behavior	Length (compared to female)	Fur
Category 1	0 - <4	No swimming or diving	<50%	Dense natal fur
Category 2	4 - <8	Swimming with coordinated body movements; No diving	50-67%	Begins molting natal fur
Category 3	8 - 12	Swims and makes shallow dives[a]	68-75%	Molt complete with adult pelage

a. Dives longer than 30 seconds.

3.2.3 Energy Budgets

3.2.3.1 Energy Budget for Pups

The energy required for pup growth ($Energy_{growth}$; MJ day^{-1}) was based on the average rate of daily mass gain for seven captive sea otter pups from Alaska during the first three months postpartum. We used multilevel growth curve model analysis to generate a regression between pup weight and age as a single growth curve (Independent Variable:

Age (Days after birth); Dependent Variable: Body mass (kg); Nested Variable: Individual Pups). The result was best described by the polynomial equation: Body Mass (kg) = $1.49 - 8.65\text{x}10^{-3}(\text{Age}) + 1.98\text{x}10^{-3}(\text{Age})^2 - 2.17\text{x}10^{-5}(\text{Age})^3 + 9.28\text{x}10^{-8}(\text{Age})^4$ where age was the number of days after birth (Figure 3-2). Using this equation, we calculated the mean daily mass for a pup during the first 90 days. A mean body mass and daily mass gain (kg day^{-1}) were then calculated for each pup category (C1: Days 2-30; C2: 31-60; C3: 61-90). We assumed that the mass gain was primarily lean tissue and the tissue composition was 85% water and 15% protein (Fomon et al., 1982). $\text{Energy}_{\text{growth}}$ was calculated as: Daily mass gain (kg day^{-1}) x 15% protein (0.15) x Cost of protein synthesis (4,500 kJ kg^{-1} protein) x 0.001 MJ kJ^{-1} (Webster, 1985).

For each pup category, we calculated the daily energy expenditure for activity ($\text{Energy}_{\text{activity}}$; MJ day^{-1}) using the activity budget and the oxygen consumption (ml O_2 $\text{min}^{-1}\text{kg}^{-1}$) for each behavior based on measurements from captive pups (Tables 3-2 and 3-3; Thometz et al., 2014; Appendix B-1). $\text{Energy}_{\text{activity}}$ includes the energy expenditure for all behaviors in the daily activity budget, including resting, which is associated with thermogenesis (regulated production of heat) to offset heat loss in water. Based on the descriptions in Thometz et al., (2014), the metabolic rates for C1 pups were comparable to those for the pre-molting pups, while the metabolic rates for C3 pups were comparable to those for molting pups. We assumed that the metabolic rates for the C2 pups were an average of the pre-molting and the molting pup values. The in-air and in-water measurements were averaged, since there was no significant difference between

them. The nursing and being-groomed behaviors in pups were considered energetically similar to resting behavior.

Table 3-2. Behavioral metabolic rates for each pup category based (Adapted from Thometz et al., 2014).

Behavior	Pup Metabolic Rates					
	Category 1		Category 2		Category 3	
	ml O_2 min^{-1} kg^{-1}	kJ min^{-1} kg^{-1}	ml O_2 min^{-1} kg^{-1}	kJ min^{-1} kg^{-1}	ml O_2 min^{-1} kg^{-1}	kJ min^{-1} kg^{-1}
Resting	24.6	0.49	24.1	0.48	23.5	0.47
Swimming	31.6	0.63	31	0.62	30.4	0.61
Feeding	31.6	0.63	32.3	0.65	33	0.66
Grooming	54.1	1.09	53	1.06	51.7	1.04
Interacting	31.6	0.63	31	0.62	30.4	0.61

Table 3-3. Activity and energy budget values for each pup category. Metabolic rates for each pup category adapted from Thometz et al. (2014). Activity budgets are from Cortez et al. (in review).

Behavior	Activity Budget						Energy Budget					
	Category 1		Category 2		Category 3		Category 1		Category 2		Category 3	
	Prop. Day[a]	min	Prop. Day	min	Prop. Day	min	kJ day^{-1} kg^{-1}	Total MJ day^{-1}[b]	kJ day^{-1} kg^{-1}	Total MJ day^{-1}	kJ day^{-1} kg^{-1}	Total MJ day^{-1}
Resting	0.991	1427	0.880	1268	0.569	820	705.0	1.3 (98.8)	613.5	2.2 (83.7)	386.9	2.2 (48.6)
Swimming	0.005	7	0.069	100	0.174	251	4.4	0.0 (0.6)	61.9	0.2 (8.5)	153.0	0.9 (19.2)
Feeding	0.000	0	0.017	24	0.169	244	0.0	0.0 (0.0)	15.6	0.1 (2.1)	161.4	0.9 (20.3)
Grooming	0.001	1	0.018	26	0.029	42	0.9	0.0 (0.1)	27.3	0.1 (3.7)	43.2	0.3 (5.4)
Interacting	0.004	5	0.016	23	0.059	84	3.3	0.0 (0.46)	14.5	0.1 (2.0)	51.5	0.3 (6.5)

[a] Proportion of 24-hour period spent in each behavioral state
[b] C1 mass: 1.84 kg; C2 mass: 3.56 kg; C3 mass: 5.80 kg

The daily, mass-specific energy expenditure for each behavior (kJ $day^{-1}kg^{-1}$) was estimated as the product of the rate of oxygen consumption for that behavior, a conversion factor of 0.02 kJ $ml^{-1}O_2$ (Schmidt-Nielsen, 1997), and the total minutes spent each day devoted to that behavior (i.e., proportion of 24 h in each behavioral activity budget state multiplied by 1,440 min day^{-1}) (Yeates et al., 2007; Thometz et al., 2014). Total energetic cost for *each* behavior (MJ day^{-1}) was calculated as the product of the mass specific energy expenditure for each activity and the mean body mass for each pup category (based on the growth rate of captive pups; see above) divided by 1,000 to convert kJ to MJ (Yeates et al., 2007; Thometz et al., 2014). Finally, $Energy_{activity}$ for each pup category was calculated as the sum of the energetic costs for all behaviors.

The daily net energy expenditure ($Energy_{net}$; MJ day^{-1}) for pups was estimated as the sum of $Energy_{growth}$ and $Energy_{activity}$. Metabolizable energy ($Energy_{met}$) accounts for the Heat Increment of Feeding (HIF), which was assumed to be 10% of the total energy ingested ($Energy_{ingest}$) and was calculated using the $Energy_{net}$ ($Energy_{met} = Energy_{net} / 0.9$) (Costa and Kooyman, 1984). To calculate the digested energy ($Energy_{digest}$), urinary energy from milk consumption was assumed to be 2% of $Energy_{ingest}$ and was calculated using the $Energy_{met}$ ($Energy_{digest} = Energy_{met} /0.98$)(Oftedal and Iverson, 1987). Finally, ingested energy ($Energy_{ingest}$) was calculated by assuming an assimilation efficiency of 97% for milk ($Energy_{ingest} = Energy_{digest} / 0.97$) (Oftedal and Iverson, 1987).
We calculated the amount of milk ingested (kg day^{-1}) by dividing the $Energy_{ingest}$ (MJ day^{-1}) by the energy content of sea otter milk ($Milk_{energy}$; MJ kg^{-1}). $Milk_{energy}$ was based on the proximate composition of sea otter milk (63% water, 23% fat, 11% protein and

1% carbohydrate [lactose]) and the equation: $Milk_{energy}$ (kcal 100 g^{-1}) = 9.11 (% fat/100) + 5.86 (% protein/100) + 3.95 (% carbohydrate/100) (Jenness et al., 1981; Oftedal et al., 1983). Using the conversion factor of 0.04184 to convert kcal 100 g^{-1} to MJ kg^{-1}, $Milk_{energy}$ was 11.67 MJ kg^{-1}. Average daily milk ingestion (kg day^{-1}) for the three pup categories was calculated as the quotient of $Energy_{ingest}$ and $Milk_{energy}$.

3.2.3.2 Energy Budget for Females

For each female category, we calculated the daily energy expenditure for activity ($Energy_{activity}$; MJ day^{-1}) using the activity budget and the oxygen consumption (ml O_2 $min^{-1}kg^{-1}$) for each behavior based on measurements from captive adult sea otters (Table 3-4; Yeates et al., 2007). As with the pup energy budget, $Energy_{activity}$ includes the energy expenditure for all behaviors in the daily activity budget, including resting which is associated with thermogenesis (regulated production of heat) to offset heat loss in water. Pup grooming behavior by females was considered energetically similar to self-grooming. When calculating the energy for swimming, the routine swimming speed for females with pups in Simpson Bay was not as energetic as that assumed by Yeates et al., (2007) and originally measured by Williams (1989). Therefore, a linear regression was calculated using the resting metabolic rate (13.3 ml O_2 kg^{-1} min^{-1}) at a speed of 0 m s^{-1} and the previously measured value of surface swimming at 0.8 m s^{-1} (29.6 ml O_2 kg^{-1} min^{-1}), which was best described by the linear regression (Surface Swimming Metabolic Rate = 13.5 + 20.1(Speed) (Williams 1989). The normal speed of swimming for female

sea otters with pups was estimated to be 50% of that observed by Williams (1989), and the energetic cost at 0.4 m s^{-1} was estimated to be 21.5 ml O_2 kg^{-1} min^{-1}.

The mass-specific energy expenditure for each behavior (kJ day^{-1} kg^{-1}) was estimated as the product of the rate of oxygen consumption for a behavior, a conversion factor of 0.02 kJ $ml^{-1}O_2^{-1}$ (Schmidt-Nielsen, 1997), and the total minutes spent each day devoted to that behavior (i.e., proportion of 24 h in each behavioral state from the activity budget multiplied by 1,440 min day^{-1})(Yeates et al., 2007). Total energetic cost for *each* behavior (MJ day^{-1}) was calculated as the product of the mass-specific energy expenditure for each activity and a mean body mass of 20 kg (Scheffer, 1951; Garshelis et al., 1986; Rotterman and Monnett, 2002; Ballachey et al., 2003) divided by 1,000 to convert kJ to MJ (Yeates et al., 2007). Finally, $Energy_{activity}$ for each female category was calculated as the sum of the energetic costs for all behaviors.

Since the energy ingested by the pup is supplied entirely from the female, the energetic cost of lactation ($Energy_{lactation}$) was calculated using the ingested energy intake of the pup (see $Energy_{ingest}$ for pups) and a lactation efficiency (i.e., efficiency of the conversion of food energy or body reserves into milk energy) of 0.80 ($Energy_{lactation}$ = Pup $Energy_{ingest}$ / 0.80; Prentice and Prentice 2008). The net energy ($Energy_{net}$) for females was estimated as the sum of $Energy_{activity}$ and the $Energy_{lactation}$. As with sea otter pups, metabolizable energy ($Energy_{met}$) accounted for the Heat Increment of Feeding (HIF), which was assumed to be 10% of her $Energy_{ingest}$ and was calculated from the $Energy_{net}$ ($Energy_{met}$ = $Energy_{net}$ / 0.9; Costa and Kooyman, 1984). To calculate digested energy ($Energy_{digest}$) for the females, urinary energy was assumed

to be 10% of her $Energy_{ingest}$, and $Energy_{digest}$ was calculated using $Energy_{met}$ ($Energy_{digest} = Energy_{met}/0.9$; Costa, 1982). Lastly, ingested energy ($Energy_{ingest}$) was calculated by assuming an assimilation efficiency of 82% ($Energy_{ingest} = Energy_{digest} / 0.82$; Costa, 1982). Daily food ingestion (kg) was calculated by dividing the $Energy_{ingest}$ (MJ day^{-1}) by the average energy content of bivalves (3.42 MJ kg^{-1}) from Simpson Bay determined by bomb calorimetry (Appendix C-1).

3.2.4 Data Analyses

Multivariate analysis of covariance (MANCOVA) was used to test for correlations between female and pup energy expenditure per behavior (dependent variables) due to the pup category (independent variable) controlling for any differences within years (covariate) using SPSS (Version 15 statistical software, Chicago, IL) at $\alpha = 0.05$. The differences in mean energy spent among the behaviors was tested for each category of pup using Turkey HSD post hoc tests.

Table 3-4. Activity and energy budgets for each female category. Female metabolic rates for each behavior are adapted from Yeates et al. (2007). Activity budgets are from Cortez et al. (in review).

Behavior	Female Metabolic Rates		Activity Budget						Energy Budget					
			Category 1		Category 2		Category 3		Category 1		Category 2		Category 3	
	ml O_2 min^{-1} kg^{-1}	kJ min^{-1} kg^{-1}	Prop. Day[a]	min	Prop. Day	min	Prop. Day	min	kJ day^{-1} kg^{-1}	Total MJ day^{-1}	kJ day^{-1} kg^{-1}	Total MJ day^{-1}	kJ day^{-1} kg^{-1}	Total MJ day^{-1}
Resting	13.3	0.27	0.504	725	0.525	756	0.458	659	195.9	3.9 (35.5)	204.0	4.1 (37.7)	177.9	3.6 (33.0)
Swimming	22	0.44	0.215	309	0.159	229	0.082	118	136.5	2.7 (24.8)	100.6	2.0 (18.6)	52.0	1.0 (9.6)
Feeding	21.6	0.43	0.085	122	0.132	190	0.325	467	52.6	1.1 (9.5)	81.8	1.6 (15.1)	201.0	4.0 (37.3)
Grooming	29.4	0.59	0.194	279	0.172	248	0.090	130	164.5	3.3 (29.8)	146.3	2.9 (27.0)	76.7	1.5 (14.2)
Interacting	24.5	0.49	0.003	4	0.012	17	0.045	65	2.1	0.4 (0.4)	8.5	0.2 (1.6)	32.0	0.6 (5.9)

[a] Proportion of 24-hour period spent in each behavioral state

3.3 Results

3.3.1 Energy Budget for Pups

Based on the mean growth rate of captive sea otters pups in Alaska (Figure 3-2), we estimated the growth rate of C1 pups (1.84 kg mean body mass) during the first 30 days after birth to be 35.0 g day^{-1}. This growth rate was non-linear and slower during the first 15 days of age (18.1 g day^{-1}) compared to the second 15 days (50.8 g day^{-1}). After 30 days, the growth rate became more linear and increased. We estimated the mean growth rate of C2 pups (3.56 kg mean body mass) to be 70.2 g day^{-1}, twice the value for the less mature C1 pups. The estimated growth rate of C3 pups (5.80 kg mean body mass) increased slightly to 79.8 g day^{-1}. Based on the assumptions described above, the $Energy_{growth}$ was 0.0236 MJ day^{-1}, 0.0474 MJ day^{-1} and 0.0539 MJ day^{-1} for C1, C2 and C3 pups, respectively (Table 3-5).

The estimated $Energy_{activity}$ for C1 pups was 1.31 MJ day^{-1} of which 99% was associated with resting (this included nursing and being groomed, which we assumed had the same metabolic cost as resting), and 1% was associated with attempted swimming or self-grooming and interacting (Table 3-3; Figure 3-3). The estimated $Energy_{activity}$ for C2 pups was 2.61 MJ day^{-1} of which 84% was associated with resting equivalent behaviors (i.e., resting, being groomed and nursing as with the C1 pup) (Figure 3-3; Table 3-3). With the development of swimming, grooming and feeding behaviors, 8% of their $Energy_{activity}$ was spent swimming, 4% grooming and 2% feeding on solid food. C2 pups also began interacting, which represented 2% of $Energy_{activity}$. The estimated $Energy_{activity}$ for C3 pups was 4.62 MJ day^{-1} of which 49% was associated

with resting equivalent behaviors, which was similar to that for the adult females (Figure 3-3; Table 3-3). C3 pups were capable of swimming, which represented 19% of $Energy_{activity}$. Although grooming and feeding behaviors were still developing, 20% of the $Energy_{activity}$ was associated with shallow foraging dives and 5% with grooming. C3 pups interacted with the female and other otters, which represented 6% of the $Energy_{activity}$.

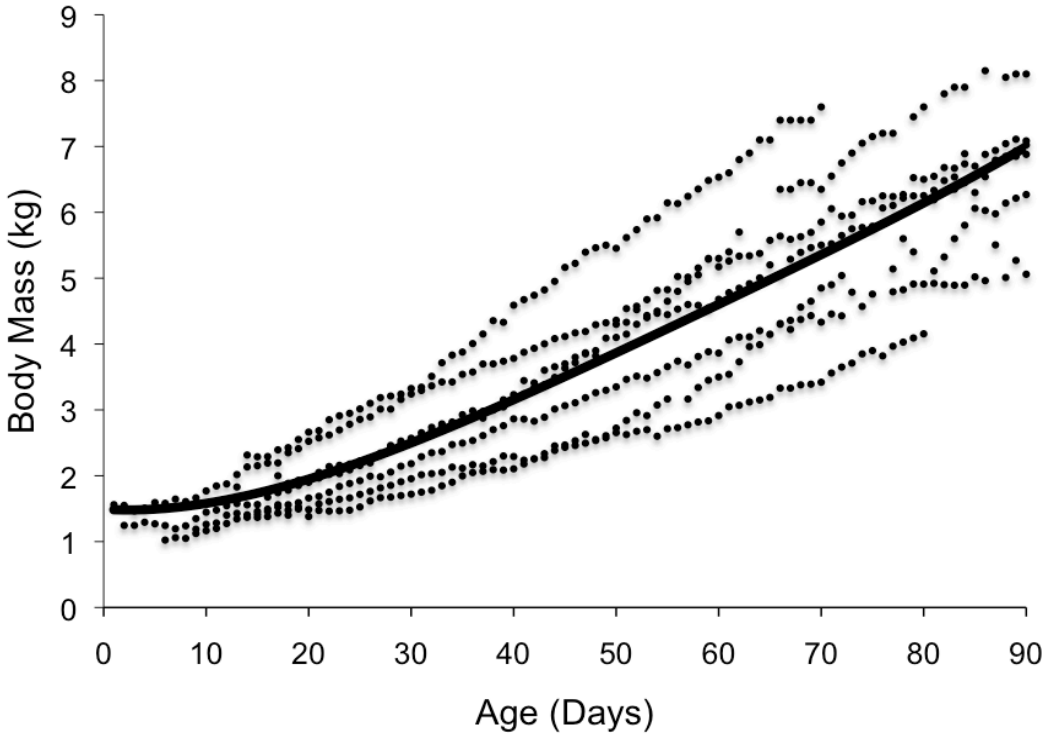

Figure 3-2. Growth curve compiled from body masses of captive sea otter pups (scatterplot) and an average growth (line) which was best described by the equation: a. Body Mass = $1.49 - 8.65x10^{-3}(Age) + 1.98x10^{-3}(Age)^2 - 2.17x10^{-5}(Age)^3 + 9.28x10^{-8}(Age)^4$

Table 3-5. Energy for activity ($Energy_{activity}$) and growth ($Energy_{growth}$) for the three categories of pups. Calculated net energy ($Energy_{net}$), metabolized energy ($Energy_{met}$), digested energy ($Energy_{digest}$) and ingested energy ($Energy_{ingest}$) as well as daily milk ingestion. Energy values are in units of MJ day^{-1} and milk consumption in units of g day^{-1}.

Category	$Energy_{activity}$ (MJ day^{-1})	$Energy_{growth}$ (MJ day^{-1})	$Energy_{net}$[a] (MJ day^{-1})	$Energy_{met}$[b] (MJ day^{-1})	$Energy_{digest}$[c] (MJ day^{-1})	$Energy_{ingest}$[d] (MJ day^{-1})	Daily Milk Ingestion[e] (g day^{-1})
1	1.31	0.024	1.34	1.48	1.51	1.56	134
2	2.61	0.047	2.65	2.95	3.01	3.10	266
3	4.62	0.054	4.67	5.19	5.30	5.46	468

a. $Energy_{net} = Energy_{act} + Energy_{growth}$
b. $Energy_{met} = Energy_{net} / 0.9$ (HIF)
c. $Energy_{digest} = Energy_{met} / 0.98$ (Urinary Energy)
d. $Energy_{ingest} = Energy_{digest} / 0.97$ (Assimilation Efficiency of Milk)
e. With an assumption of a pup exclusively nursing

The $Energy_{ingest}$ for a C1 pup was 1.56 MJ day^{-1}, which increased 2-fold to 3.10 MJ day^{-1} for a C2 pup and a further 1.8-fold to 5.46 MJ day^{-1} for a C3 (Table 3-5; Figure 3-4). Daily milk ingestion for C1, C2 and C3 pups was 134, 266 and 468 g $day^{-1,}$ respectively, which was 7-8% of mean body mass (Figure 3-5).

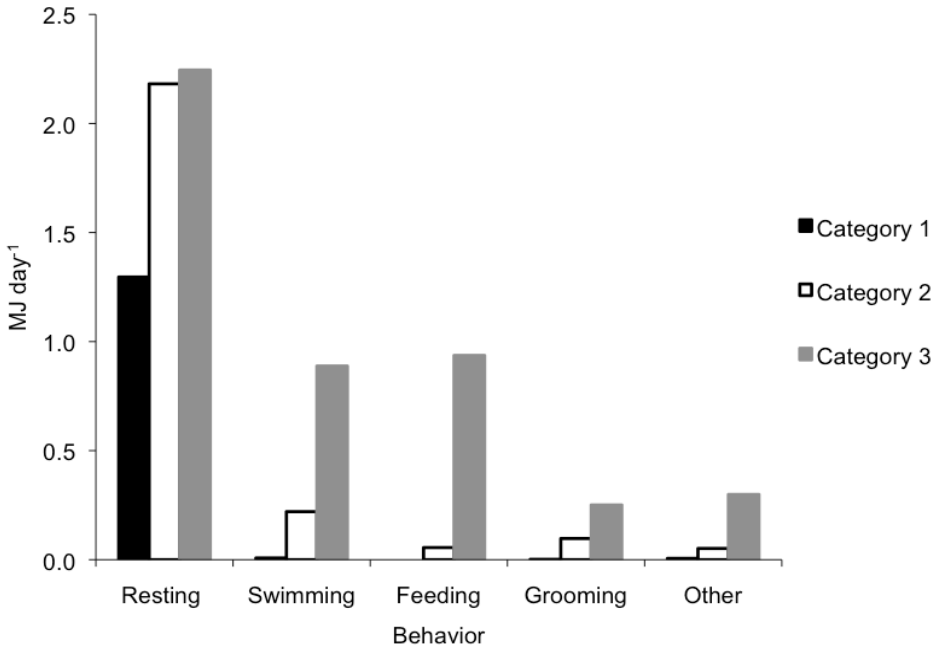

Figure 3-3. Energy expenditure (MJ day^{-1}) as a function of behavior for Category 1, Category 2, Category 3 sea otter pups

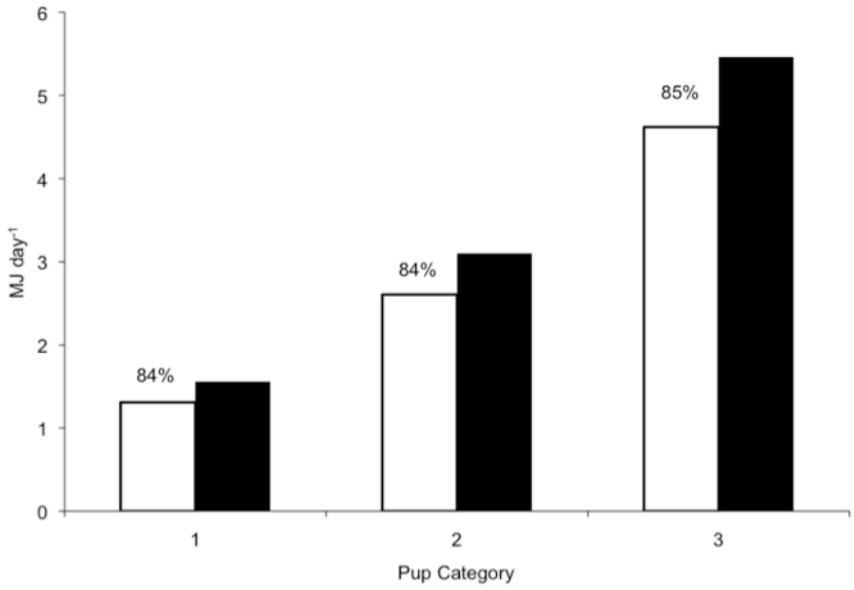

Figure 3-4. Comparison of pup $Energy_{activity}$ (white bars) and the $Energy_{ingest}$ (black bars) in MJ day^{-1} and as a percentage of $Energy_{ingest}$.

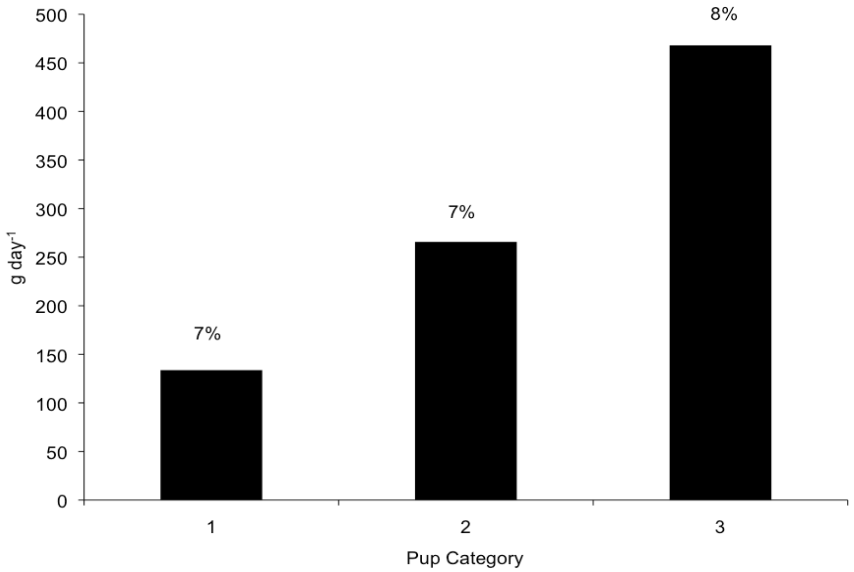

Figure 3-5. Daily milk ingestion (g day^{-1}) and as a percentage of body mass for the three pup categories.

The MANCOVA showed a significant ($P < 0.0001$) difference in the energy associated with each behavior among the three pup categories. The amount of energy associated with each behavior was also significantly different among pup categories (resting: $P < 0.0001$; self-grooming: $P < 0.0001$; being groomed: $P < 0.0001$; feeding: $P < 0.0001$; being groomed: $P < 0.003$; swimming: $P < 0.0001$, nursing: $P < 0.0001$, interacting: $P < 0.0001$). A Turkey post-hoc test showed that the energy expended by C1 pups in each behavior was significantly different from that for C2 and C3 pups.

3.3.2 Energy Budget for Females

The $Energy_{activity}$ for C1, C2 and C3 females were nearly identical (only 2.2% difference), although the allocation of energy to particular behaviors differed. The estimated $Energy_{activity}$ for a C1 female was 11.03 MJ day^{-1} of which 36% was associated with resting, 30% with self-grooming and pup grooming, 25% with swimming, 10% with feeding and <1% with interacting (Table 3-4; Figure 3-6). The estimated $Energy_{activity}$ for a C2 female was 10.82 MJ day^{-1} with the primary difference in energy allocation resulting from an increase associated with feeding (15%) and a decrease with swimming (19%) (Table 3-4; Figure 3-6). Energy expenditure associated with resting (38%) and self-grooming and pup grooming (27%) was similar to that for a C1 female. The estimated $Energy_{activity}$ for a C3 female was 10.79 MJ day^{-1} with less energy allocated to swimming (10%) and much more (37%) to feeding than C1 and C2 females (Table 3-4; Figure 3-6). The energy expenditure associated with resting decreased

slightly (33%), while that for self-grooming and pup grooming (14%) was about half that for C1 females.

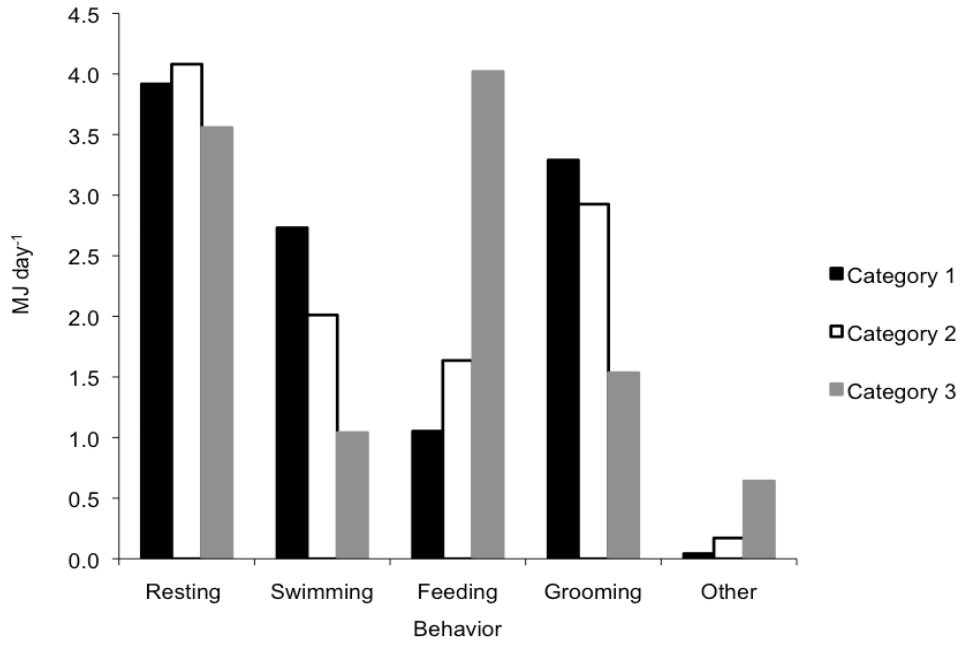

Figure 3-6. Energy expenditure as a function of behavior for the three categories of females. Grooming behavior includes self-grooming and pup grooming.

$Energy_{lactation}$ for a C1 female was the lowest of all the females at 1.95 MJ day^{-1}, because C1 pups were small and had the slowest growth rate (35 g day^{-1}) (Table 3-6; Figure 3-7A). Although the $Energy_{activity}$ for a C2 pup was similar to that for a C1 pup, the growth rate for a C2 pups doubled (70 g day^{-1}), and the $Energy_{lactation}$ increased to 3.88 MJ day^{-1}. The growth rate for a C3 pup (80 g day^{-1}) was similar to that for a C2 pup, but the $Energy_{activity}$ for a C3 pup increased significantly. As a result, the $Energy_{lactation}$ for a C3 female increased to 6.83 MJ day^{-1}. The $Energy_{ingest}$ for a C1

female was 19.55 MJ day^{-1}, which increased to 22.13 MJ day^{-1} for a C2 female and 26.53 MJ day^{-1} for a C3 female (Table 3-6; Figure 3-7B). The daily food ingestion for a C1 female was 5.72 kg day^{-1}, which was 29% of body mass for a 20 kg female (Table 3-6; Figure 3-8). A C2 female ingested 6.47 kg day^{-1} (32% of body mass), and a C3 female ingested 7.76 kg day^{-1} (39% of body mass).

The MANCOVA showed there was a significant difference in energy expenditure for each female category associated with grooming ($P < 0.0001$), feeding ($P < 0.0001$), swimming ($P < 0.0001$) and interacting ($P < 0.0001$). The Turkey post hoc tests showed that there was a significant decrease in the amount of energy associated with pup grooming for all female categories. The C1 and C2 females allocated similar amounts of energy for interacting and feeding, which differed significantly from that for C3 females. The energy associated with swimming differed among the three female categories.

Table 3-6. Energy for activity ($Energy_{activity}$) and lactation ($Energy_{lactation}$) for the three categories of females. Calculated net energy ($Energy_{net}$), metabolized energy ($Energy_{met}$), digested energy ($Energy_{digest}$) and ingested energy ($Energy_{ingest}$) as well as daily milk ingestion. Energy values are in units of MJ day^{-1}.

Category	$Energy_{activity}$ (MJ day^{-1})	$Energy_{lactation}$ [a] (MJ day^{-1})	$Energy_{net}$ [b] (MJ day^{-1})	$Energy_{met}$ [c] (MJ day^{-1})	$Energy_{digest}$ [d] (MJ day^{-1})	$Energy_{ingest}$ [e] (MJ day^{-1})
1	11.03	1.95	12.98	14.43	16.03	19.55
2	10.82	3.88	14.70	16.33	18.15	22.13
3	10.79	6.83	17.62	19.58	21.75	26.53

a. $Energy_{Lactation} = Energy_{pup\ ingest} / 0.8$ (Lactation Efficiency)
b. $Energy_{net} = Energy_{act} + Energy_{Lactation}$
c. $Energy_{met} = Energy_{net} / 0.9$ (HIF)
d. $Energy_{digest} = Energy_{met} / 0.9$ (Urinary Energy)
e. $Energy_{ingest} = Energy_{digest} / 0.82$ (Assimilation Efficiency of Clams)

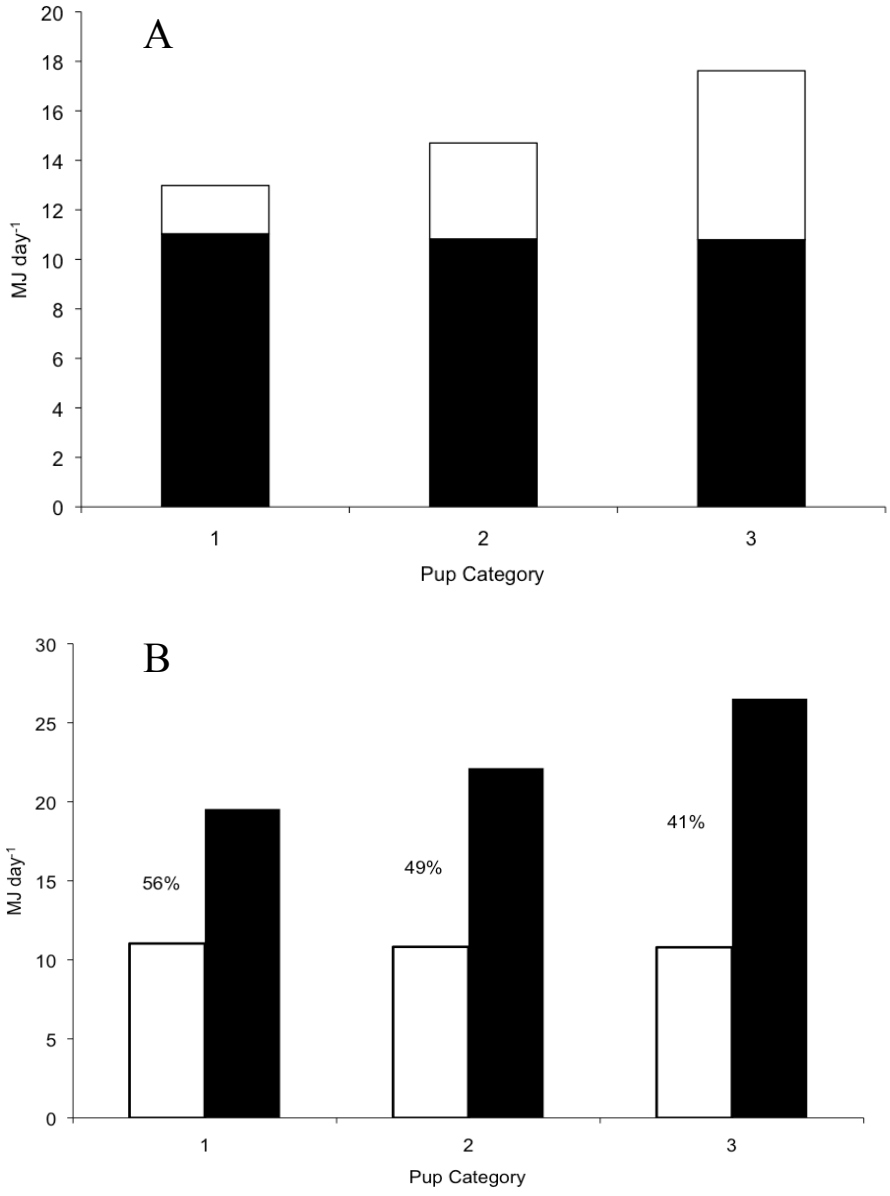

Figure 3-7. A) Female $Energy_{net}$ (MJ day^{-1}) divided into $Energy_{activity}$ (black bar) and $Energy_{lactation}$ (white bar); B) Comparison of female $Energy_{ingest}$ (black bars) and the $Energy_{activity}$ (white bars) which accounts for about half of the total ingested energy.

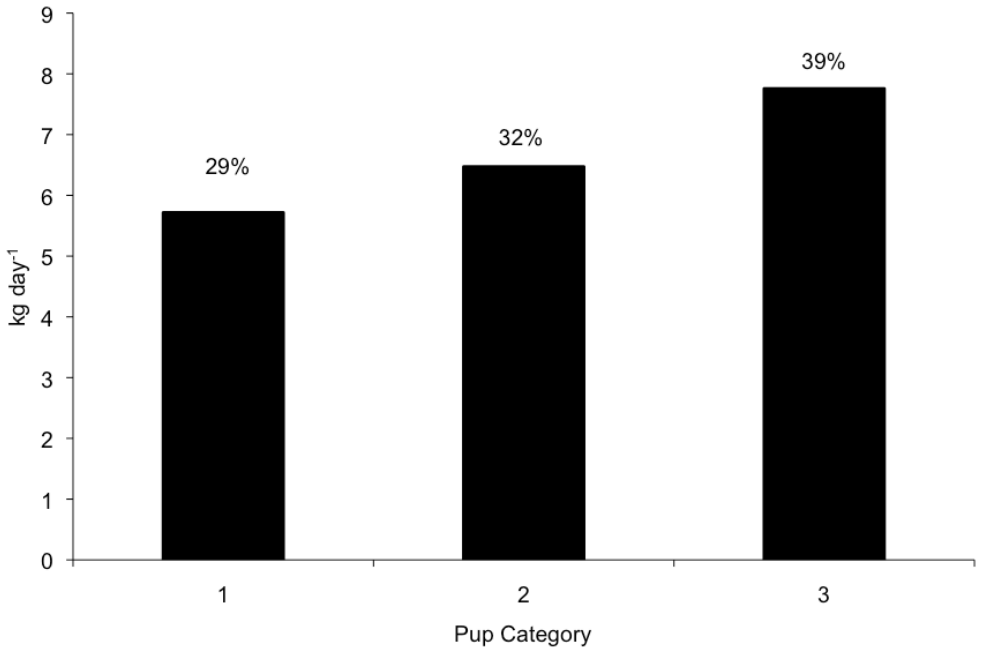

Figure 3-8. Daily food consumption (kg day^{-1}) and as a percentage of body mass for a 20 kg female.

3.4 Discussion

3.4.1 Energy Budget for Pups

In young mammals, energy is required for activity and growth, so competing energetic demands exist that do not occur in mature mammals. Mature sea otters already have a resting metabolic rate that is 2.6-fold greater than the allometric prediction for terrestrial carnivores (McNab, 2008). Sea otter pups have a resting metabolic rate (29.4 kJ hr^{-1} kg^{-1} for a body mass of 1.84 kg; 3- 2, Thometz et al., 2014) that is 1.8-fold greater than an adult otter (16.2 kJ hr^{-1} kg^{-1} for a body mass of 27.3 kg; Table 3-2, Yeates et al., 2007).

However, if we use the allometric mass specific scaling factor of 0.75 for carnivores (McNab, 2008), then sea otter pups have a resting metabolic rate (34.2 kJ hr^{-1} $kg^{-0.75}$) that is similar (9% less) to adults (36.7 kJ hr^{-1} $kg^{-0.75}$). Relative to other neonatal mammals, sea otter pups have an average scaled resting metabolic rate that is 2.4-fold (range 1.8-3.0) greater than neonatal dogs (13.4 kJ hr^{-1} $kg^{-0.75}$; Crighton and Pownall, 1974), rhesus monkeys (14.9 kJ hr^{-1} $kg^{-0.75}$; Dawes et al., 1960), sheep (19.4 kJ hr^{-1} $kg^{-0.75}$; Dawes and Mott, 1959) and humans (11.4 kJ hr^{-1} $kg^{-0.75}$; Hill and Rahimtulla, 1965). Hence, the 2.6-fold increase in resting metabolic rate in adult sea otters relative to adult carnivores is similar to the 2.4-fold increase in resting metabolic rate of sea otter pups relative to neonatal dogs, rhesus monkeys, sheep and humans. However, relative to neonatal northern fur seals (30.7 kJ hr^{-1} $kg^{-0.75}$; Donohue et al., 2000), harbor seals (22.4 kJ hr^{-1} $kg^{-0.75}$; Burns et al., 2005) and northern elephant seals (31.1 kJ hr^{-1} $kg^{-0.75}$; Rea and Costa, 1992), the resting metabolism of neonatal sea otters is only slightly (20%) higher.

The elevated resting metabolic rate in neonatal sea otters results primarily from thermogenesis (regulated production of heat) necessary for the thermoregulation in the marine environment. Basal metabolism is so high that it represents a large percentage of the average energetic cost of other behaviors for all age categories of pups: 77% of swimming, 74% of feeding, 45% of grooming and 77% of interacting. With regards to the daily Field Metabolic Rate (FMR; MJ day^{-1}), the underlying resting metabolic rate for all behaviors represents 100% of $Energy_{ingest}$ for C1, 94% for C2 and 85% for C3

pups. Hence, thermogenesis dominates the metabolism of sea otter pups, which indicates the vital role it plays in the survival of the smallest endothermic neonate born at sea.

Compared to $Energy_{activity}$, the $Energy_{growth}$ is only 1-1.5% of $Energy_{ingest}$ in C1 (0.024 MJ day^{-1}), C2 (0.047 MJ day^{-1}) and C3 pups (0.054 MJ day^{-1}) (Table 3-5). Sea otter pup growth is similar to that in fur seals and sea lions. These neonatal otariids grow slowly over a period of 4-12 mo and mainly acquire lean tissue as opposed to fat (Oftedal et al., 1987; Georges et al., 2001; Bowen et al., 1992). Otariid pups usually grow at 60 to 380 g day^{-1}, which is significantly less than the growth rate of phocid pups (800-7,000 g day^{-1}) (Boness and Bowen, 1996). Compared to the elevated growth rates in pinnipeds, growth rates of chimpanzees (12-13 g day^{-1}), gorillas (16 g day^{-1}), and humans (7.7 g day^{-1}) are minor (Case, 1978b). Growth rates from birth to weaning of wild sea otter pups in Prince William Sound averaged 83 g day^{-1} and 95 g day^{-1} for female and male pups, respectively (Monnett et al., 1991). The captive pups in this study grew at 35 g day^{-1} as C1 pups, which increased to 70.2-79.8 g day^{-1} in the C2 and C3 pups, respectively. Similar to C1 pups, Northern fur seal pups have a very slow growth rate during the perinatal period (1-10 days). Since fur seals are born with minimum body fat and a neonatal pelage with poor insulating qualities, most of the youngest pups' metabolism is associated with thermogenesis instead of growth (Boltnev et al., 1998). The highest growth rates recorded in these fur seals occurred in preweaning pups after molting as they acquired body fat (Boltnev et al., 1998). Like the preweaning Northern fur seal pups, C3 pups that have molted their natal pelt also have a higher growth rate.

3.4.2 Sea Otter Pup Behavioral Development

As the most altricial mammal born at sea, C1 sea otter pups are totally dependent on the females for survival. These very small pups spent most of their time in resting equivalent behaviors, including resting, nursing or being groomed, and lacked the strength or coordination for swimming, feeding or self-grooming. The absence of highly energetic behaviors resulted in a relatively low $Energy_{activity}$ (1.31 MJ day^{-1}) compared with C2 and C3 pups. The $Energy_{ingest}$ for C1 pups (1.56 MJ day^{-1}) was provided entirely by milk (134 g milk day^{-1}); therefore, requiring minimal work for C1 pups to feed (Payne and Jameson, 1984). By minimizing $Energy_{activity}$, the pups can allocate more energy to thermogenesis and growth (Gaillard et al., 1997; Koteja, 2000).

Lactose and fat in sea otter milk provide energy, while the protein is essential for growth (Jenness, 1986). For the first 90 days, the pups consumed 7-8% of their body mass in milk. Sea otter milk is 62% water, and its dry mass is composed of about 61% fat, 29% protein and 0.03% lactose (Jenness et al., 1981; Oftedal, 1984). Pinniped milk is 49-59% water and has little or no lactose, while the fat concentration is higher (~74-82%) and protein concentration is lower (11-22%) based on dry mass (Oftedal, 1984). Terrestrial carnivore milk, which is 18-34% dry mass, usually contains 7-25% lactose, 32-55% fat (the highest being from the brown bear) and 25-38% protein (Oftedal, 1984). Hence, the composition of sea otter milk is similar to that of pinnipeds with a slightly lower fat content. However, the amount of protein in sea otter milk is similar to that of terrestrial carnivores. Since sea otter pups use fur for thermo-insulation, fat does not accumulate as a blubber layer, and the elevated protein levels can be used for growth.

As the young mammals grow, their energy requirements increase, and the energetic cost of milk production by the female increases (Kunz, 2004). C2 pups consumed 266 g milk day^{-1} with an $Energy_{ingest}$ of 3.1 MJ day^{-1}, which was largely associated with the increase in $Energy_{activity}$ (2.61 MJ day^{-1}). Even though 84% of their energy expenditure was allocated to resting equivalent behaviors, there was an additional expenditure of energy due to swimming (~8%). Feeding and the self-grooming behaviors also began to develop in C2 pups, although only 2% and 4% of the energy expenditure was used for these behaviors, respectively. In addition, these pups began to molt their natal pelage (Payne and Jameson, 1984) and swim alongside the females making short, shallow dives while the females were foraging (Cortez et al., in review). C2 pups began to solicit food from the female, and this behavior continues until weaning (Payne and Jameson, 1984). Solid food provided by the female for C2 and C3 pups supplements milk energy, and this transition usually coincides with the peak lactation period (Langer, 2008).

The $Energy_{activity}$ for C3 pups was 4.62 MJ day^{-1} with 49% associated with resting behavior similar to the females. By 8-10 weeks, the pups were strong swimmers in both the prone and supine position and began diving with the foraging females (Payne and Jameson, 1984). About 19% of their energy was allocated to swimming and 20% to feeding, which corresponded to the increase in $Energy_{activity}$. C3 pups also began to capture small prey items in conjunction with the female. C3 pups had an $Energy_{ingest}$ of 5.46 MJ day^{-1}. If we assume that all energy came from nursing, then these pups would have consumed 468 g milk day^{-1}. However, there was a minor contribution of solid food

to the C2 and C3 pup's diet. 17% of prey captured by C2 females was shared with their pups, which increased to 25% for C3 females (M Cortez unpublished data). Regardless of the increasing contribution of solid food to the diets of C2 and C3 pups, most of the $Energy_{ingest}$ still came from milk energy. In addition, 7% of the day was spent nursing, similar to C1 and C2 pups, and C3 pups may become more efficient at consuming milk in the same amount of time, which has been seen in other mammals (i.e. stellar sea lion pups, northern fur seals, human babies, and horse foals) (Costa and Gentry, 1986; Higgins et al., 1988; Blaxter, 1989; Cameron, 1998).

3.4.3 Energy Budget for Females

With pup mortality occurring predominantly during the first 60 days after birth (Siniff and Ralls, 1991, Riedman et al., 1994; Monnett and Rotterman, 2000), neonatal care is critical and reflected in the females' activity budget. The female not only feeds the pup but also protects it from environmental and predatory threats while maintaining the insulating properties of its fur for thermoregulation (Cortez et al., in review). The provisioning of offspring during lactation is an energetically and nutritionally expensive process, which is also correlated with some of the highest daily energetic expenditures (Mellish et al., 2000; Langer, 2008).

As mentioned above, mature sea otters have a resting metabolic rate that is 2.6-fold greater than the allometric prediction for terrestrial carnivores (McNab, 2008), and this increase is derived primarily from thermogenesis (regulated production of heat) necessary for thermoregulation in the marine environment. As with pups, the basal

metabolism of adult females is so high that it represents a large percentage of the average energetic cost of other behaviors: 61% of swimming, 63% of feeding, 46% of grooming and 55% of interacting. With regards to the daily Field Metabolic Rate (FMR; MJ day^{-1}), the underlying basal metabolic rate for all behaviors represents 70% of $Energy_{ingest}$ for C1 females and 72% for C2 and C3 females. Hence, thermogenesis dominates the metabolism of female sea otters as with their pups.

Overall, there was little difference in the $Energy_{activity}$ (range 10.79-11.03 MJ day^{-1}) for the three categories of females, although their activity and energy budgets were very different. There was little difference in the daily energy expenditure associated with resting, while the energy expenditures associated with swimming and grooming (self-grooming and pup grooming together) decreased as the pups matured. The daily energy expenditure for feeding increased as the demands from the pup increased. C1 females in Simpson Bay expended 2.73 MJ day^{-1} (25% of $Energy_{activity}$) in swimming around the study area carrying their pups, often making long, meandering loops that brought them back to the same location without any apparent reason. We can only speculate about the cause of this behavior, but it may be related to predator avoidance. By reducing the time that newborn pups are left unattended at the surface and by moving around the study area, females may be engaging in avoidance of predators (i.e., bald eagles; Cortez et al., in review). The energy expended in meandering swimming decreased to 2.01 MJ day^{-1} (19% of $Energy_{activity}$) for C2 females and 1.04 MJ day^{-1} (10 % of $Energy_{activity}$) for C3 females as the pups grew and the potential threat of bald eagle predation diminished.

The mass-specific metabolic rate of small mammals is much higher than that of larger mammals; therefore, smaller animals are unable to store enough energy as fat to compensate for long periods of fasting (Oftedal, 2000). Lactation is the most expensive reproductive stage that is associated with an increase in foraging effort by up to 30% in larger species (Gittleman and Thompson, 1988). Lactating Northern fur seal females can consume 80% more food than a non-lactating female (Costa, 1993). Even though elephant seals are capital breeders, females need to increase their foraging effort by 10% to store sufficient energy prior to the mother's fasting period for lactation (Costa et al., 1983). In terrestrial animals, increases in energy intake during lactation can be as high as 48% in pine voles or 160% in red deer (Costa et al., 1986).

As the sea otter pups matured, their energy needs increased. With this elevated energy requirement from the pups, the females foraging effort also increased and the energy allocated towards other activities, such as swimming at the surface, decreased. The energy expended in feeding increased from 1.05 MJ day^{-1} (10% of $Energy_{activity}$) for C1 females to 4.02 MJ day^{-1} (37% of $Energy_{activity}$) for C3 females. This increase was associated with an elevated $Energy_{lactation}$, which increased from 1.95 MJ day^{-1} (10% of $Energy_{ingest}$) in C1 females to 8.83 MJ day^{-1} (26% of $Energy_{ingest}$) in C3 females. Since the lactation efficiency is 80%, most of the cost to the female is in the energetic content of the milk, which comes from the diet (i.e., $Energy_{ingest}$). The $Energy_{ingest}$ for C1 females increased to 22.13 and 26.53 MJ day^{-1} for C2 and C3 females. C1 females consumed 5.72 kg prey day^{-1} (29% of body mass or ca. 560 clams day^{-1}), while C2 females consumed 6.47 kg (32% of body mass or ca. 634 clams day^{-1}). C3 females, which had to

support the energetic needs of a larger and more active pup, consumed 7.76 kg prey day^{-1} (39% of body mass or ca. 760 clams day^{-1}).

Water conducts heat 25-fold faster than air, which makes sea otters susceptible to hypothermia in the cool waters of the North Pacific. Sea otters rely entirely on fur that traps an air layer next to the skin and provides 70% of the thermal insulation (Kenyon 1969; Costa and Kooyman 1982; Davis et al., 1988; Williams et al., 1992). The marine otter (*Lontra felina*) is exclusively marine like the sea otter and also has no body fat, however they offset heat loss by reducing the time spent in the water (Estes, 1986; Vianna et al., 2010; Valqui, 2012). More than 80% of their time is spent in the dens and mainly only go to the water to feed (Vianna et al., 2010; Valqui, 2012).

In contrast, most marine mammals rely on blubber for thermal insulation, so grooming is not required. To maintain this air layer, sea otters felt and aerate their fur by grooming, a behavior that is critical for maintaining a stable core body temperature (Costa and Kooyman 1982; Williams et al., 1988; Davis et al., 1988). Pups do not acquire the dexterity to efficiently groom themselves until around their eighth week of age (Payne and Jameson, 1984). Therefore, they depend on the female for most of the fur maintenance during the first few months of life (Kenyon 1975; Hanson et al., 1993). This activity decreases as pups mature and acquire the ability to self-groom. Hence, the energy expended by females to groom the pups decreased from 3.29 MJ day^{-1} (30% of $Energy_{activity}$) for C1 females to 1.53 MJ day^{-1} (14% of $Energy_{activity}$) for C3 females. The decrease in energy devoted to grooming in C3 pups coincided with the ability to self-groom and the molt of their lanugo and its replacement with adult fur.

3.4.3.1 Catabolism of Body Tissue

The reliance on energy stores as fat is evident across different taxa of mammals. Black and brown bears (Order Carnivora, Family Ursidae) fast for periods of 4-5 months (from 1 mo prior to parturition to 2-3 mo postpartum). Lactating polar bears fast for as long as 8 mo (Oftedal, 2000). Pregnant blue whales and fin whales acquire a large blubber layer that can represent 38% and 25% of their body mass during their foraging season (Oftedal, 2000). However, even these large body energy reserves may not even be sufficient for the entire course of lactation. Larger phocids can support their daily energy requirements for lactation entirely through fat, while smaller phocids (e.g., harbor seals) must feed during the latter part of lactation (Oftedal, 2000). Otariid females are income-breeders; therefore, they only rely on body fat for about 5-9 days after parturition and then make regular foraging trips throughout lactation (Oftedal, 2000).

C1 females forage, on average, only 2 hr each day (Cortez et al., in review), which represents 9% of the daily activity budget during the first month postpartum. This decrease in foraging behavior has been observed in females with young pups in other parts of Alaska and California (Gelatt et al., 2002; Thometz et al., 2014). The calculated $Energy_{ingest}$ for C1 females (19.55 MJ day^{-1}) was based on the combined energetic requirements of the female and pup, and it was assumed that all of the energy came from the diet. The ability of the C1 female to obtain around 5.72 kg of food (ca. 560 clams or 8 clams $dive^{-1}$) in only 2 hr time (average female dive duration: 1.69 min) is difficult to reconcile with normal feeding behavior of sea otters without pups (Wolt et al., 2012). However, pregnant females may develop some subcutaneous fat in the dorsal caudal area

(R.W. Davis unpublished data), and otherwise healthy lactating or pregnant females that have died from boat strikes in Kachemak Bay, Alaska had abundant mesenteric fat in the omental bursa, renal fat around the kidneys and a large fat deposit in the inguinal area (V.A. Gill unpublished data; Appendix D-1). As with otariids, these body fat stores may allow females to reduce foraging without entering a state of starvation and devote more time to caring for their pups during the critical first two weeks when the neonate is very vulnerable to hypothermia and predation. If we assume that 50% of the $Energy_{ingest}$ comes from body fat stores instead of the diet during the first 14 days postpartum, then C1 females would use 0.13 kg fat day^{-1} (energy equivalent of fat: 39 MJ kg^{-1}; Prentice and Prentice, 1988) or a total of 1.8 kg (ca. 9% of body mass assuming a 20 kg female). This may be the explanation for the paradoxically low foraging effort observed in C1 females with vulnerable, newborn pups.

3.5 Conclusion

Neonatal C1 pups had a slow growth rate, which doubled in C2 and C3 pups although the $Energy_{growth}$ represented only 1-1.5% of $Energy_{ingested}$ for all age classes. The remainder was associated with activity. For the first four weeks of life, the pup's activity was associated primarily with resting equivalent behaviors (i.e., resting, being groomed, nursing). As they matured, the C2 and C3 pups exhibited more active behaviors such as feeding, swimming and self-grooming. The increase in $Energy_{activity}$ required an increase in the $Energy_{ingest}$. Throughout the first three months after birth,

pups must consume 7-8% of their body mass in milk, but this was supplemented increasingly with solid food in C2 and C3 pups.

Sea otter females used several strategies to compensate for the increase in energetic demands of the developing pups. As with many mammals, $Energy_{ingest}$ was 36% greater in females with C3 pups relative to those with C1 pups. This represented an increase in food consumption from 29% of body mass in C1 females to 39% of body mass in C3 females. Although the $Energy_{activity}$ was similar for all three females, C1 females devoted more energy to swimming while C3 females expended more energy in feeding. The increase in feeding effort in C3 females was needed to support the 3.5-fold increase in milk production and to assist the pup in foraging. In contrast, C1 females only fed only 9% of the day, and it is likely that they relied, at least in part, on stored body fat for metabolism and milk production during the first few weeks postpartum. Our study reveals the energetic strategies that female sea otters use to support one of the highest metabolic rates in any adult and neonatal carnivore and the extreme effort of the female to raise an altricial pup at sea.

CHAPTER IV

CONCLUSION

Parental care is essential for the early survival of most mammalian offspring (Clutton-Brock, 1991). The provisioning of young during lactation is an energetically expensive process and is also correlated with some of the highest daily energy expenditures (Mellish et al., 2000; Langer 2008). However, this is especially true for neonatal sea otters, which are the most altricial marine mammals born at sea. This study examined changes in the allocation of time and energy by females and pups during the first three months postpartum. This is a critical period as pups develop the behaviors essential for survival.

Female sea otters care for their pups without assistance from the male, and there are significant threats to the survival of pups that must be counteracted throughout the dependency period. Neonatal sea otters are born at sea and are highly susceptible to drowning. Newborn captive sea otter pups that are not groomed effectively sink shortly after death (Sherrod et al., 1975). Adult sea otters are excellent swimmers, and the females usually carry their pups on their abdomen as she swims at the surface. The pup's lanugo traps a layer of air next to the skin and makes the pup positively buoyant, so that it can rest effortlessly at the surface. Around four weeks after birth, the pups develop the ability to swim, and older C2 and C3 pups swam at the surface, usually while the female was feeding. Around six weeks, the pups that have molted their lanugo develop the

ability to make short, shallow dives (Payne and Jameson, 1984). By eight weeks, 17% of the pup's time was spent swimming and diving with the female.

Sea otter pups are born without efficient thermoregulatory capabilities. Therefore, the pups rely on their neonatal lanugo to maintain a constant body temperature of ca. 37°C (Costa and Kooyman 1982; Williams et al., 1988; Davis et al., 1988). C1 females were entirely responsible for maintaining the air layer in the pups' fur by grooming, which decreased as pups matured and developed the gradual ability to self-groom. The total time devoted to pup grooming (provided by the female and the pup) was 13% for C1 pups, 12% for C2 pups and 7% for C3 pups, with the latter being most similar to the 7% of time spent self-grooming by the females.

Without a thick blubber layer as an energy reserve, sea otters must forage daily throughout the year and are susceptible to rapid starvation if feeding is interrupted (Costa and Kooyman, 1982; Davis et al., 1988). Young sea otter pups depend on the female for milk and solid food. C1 females only fed 9% of the time, even though their pups obtained all nourishment from nursing. As the pups matured and their energy requirements increased, females increased foraging effort to feed themselves and their pups (32% as C3 females). This increase may be compensation for the lack of feeding as C1 females or may be due to the increased demand from the pup. To meet their elevated nutritional requirements, C3 pups either nursed 7% of the time, consumed 25% of the solid prey brought up by females or captured 33% of their own prey during short, shallow dives alongside the female.

Adult sea otters are susceptible to predation by killer whales and sharks, while young pups are most vulnerable to bald eagle predation. C1 females decreased foraging effort and spent more time swimming at the surface in a meandering fashion in large loops that brought them back to the same location without any apparent reason. This behavior may have been associated with female vigilance to protect young pups from eagle predation and might also explain the low percentage of the time that the female left the pup unattended at the surface (9% of the time).

Play behavior and interacting with other otters is important in young mammals, because it promotes physical conditioning, socialization and sensorimotor/cognitive skills. In addition, this behavior may create and strengthen social bonds among the young and adults (Bekoff, 1989). C1 females and pups avoided interacting with other otters, while this behavior increased in C2 and C3 pups as they matured. C3 pups were noticeably more social than the C1 and C2 pups and interacted more often with the female and other otters while the female was foraging. C3 females also permitted a larger distance between themselves and their pups allowing them to interact with otters in other rafts.

Activity budgets for females and pups based on shore-based observations were similar to those made from the skiff and recorded only a small decrease in the percentage of time spent resting and a small increase in swimming. If the skiff were affecting the otter's behavior (i.e., the otter was avoiding the skiff), we would expect the opposite result. In addition, we would expect a decrease in the amount of time feeding using boat-based methodology, but found an equivalent amount of time feeding between both

methods. Likewise, there was little or no difference in the time budgets of pups recorded from the boat or from shore. The boat-based methodology provided more detailed behavioral observations and could be used under lower light levels that enabled 24-hr activity budgets.

Thermogenesis dominates the metabolism of sea otter pups, which indicates the vital role it plays in the survival of the smallest, endothermic neonate born at sea. The $Energy_{growth}$ was only 1-1.5% of $Energy_{ingest}$ for each pup category. Growth rates from birth to weaning of wild sea otter pups in Prince William Sound average 83 g day^{-1} for females and 95 g day^{-1} for male pups (Monnett et al., 1991). In comparison, captive pups grew at 35 g day^{-1} as C1 pups, which increased to 70.2-79.8 g day^{-1} in the C2 and C3 pups, respectively. For the first 90 days, the pups consumed 7-8% of their body mass in milk. In terms of their $Energy_{activity}$, C1 pups spent most of their time in resting equivalent behaviors, including resting, nursing or being groomed, and lacked the strength or coordination for swimming, feeding or self-grooming. Even though 84% of the energy expenditure of C2 pups was allocated to resting equivalent behaviors, there was an increase in energy expenditure due to swimming (~8%), feeding (2%) and self-grooming (4%). Resting behavior in C3 pups (49% of $Energy_{activity}$) was similar to that of the females and ca. 19% of their energy was allocated to swimming and 20% to feeding.

Overall, there was little difference in the $Energy_{activity}$ (range 10.79-11.03 MJ day^{-1}) for the three categories of females, although their activity and energy budgets were very different. The energy expenditures associated with swimming and grooming decreased as the pups matured. The daily energy expenditure for feeding increased as the

demands from the pup also increased (1.05 MJ day^{-1} to 4.02 MJ day^{-1}). As the pups began to self-groom, the energy expended in pup grooming also decreased. The $Energy_{ingest}$ in females increased from 19.55 (C1) to 26.53 MJ day^{-1} (C3), which was associated with an elevated $Energy_{lactation}$ as the pup's $Energy_{activity}$ increased. C1 females consumed 29% of their body mass in food, which increased to 39% in C3 females.

The reliance on energy stored as fat is evident across different taxa of mammals. On average, C1 females foraged only 2 hr each day (Cortez et al., in review), which represents 9% of the daily activity budget during the first month postpartum. This decrease in foraging behavior has been observed in females with young pups in other parts of Alaska and California (Gelatt et al., 2002; Thometz et al., 2014). The ability of the C1 female to obtain around 5.72 kg of food during such a small amount of time is difficult to reconcile with normal feeding behavior of sea otters without pups. However, pregnant females may develop some subcutaneous fat in the dorsal caudal area (R.W. Davis unpublished data), omental bursa (mesenteric fat), renal fat around the kidneys or a large fat deposit in the inguinal area (V.A. Gill unpublished data). These body fat stores may allow females to reduce foraging without entering a state of starvation and devote more time to caring for their pups during the critical first two-to four weeks post partum when the neonate is very vulnerable to hypothermia and predation.

Generally, marine mammals show a wide range in their foraging ecology including herbivores, benthic invertebrate feeders, batch feeders, intermediate feeders and apex carnivores, and are found along coasts and in all oceans at varying depths (Kiszka et al., 2015). Therefore, they have an important top down effect on a variety of

ecosystems. In addition, sea otters, pinnipeds and polar bears have the potential to link terrestrial and marine habitats (Kiszka et al., 2015). The three subspecies of sea otter (*Enhydra lutris lutris, Enhydra lutris kenyoni, Enhydra lutris nereis*) vary in their population trends. Even within populations, there are certain habitats that have populations that are more prolific than others. Sea otter populations in Prince William Sound and Southeast Alaska are stable or increasing, while populations in the Aleutian Islands are decreasing. Reasons for the decline in the Aleutian Islands are unknown, but are believed to be due to killer whale predation. The decline or failure of the population of sea otters in California may be due to a decrease in prey availability, shark predation or disease, for example infections from *toxoplasma gondii*. The high metabolic rates and prey consumption of sea otters make them an important species in shaping community structure in different habitats. For a population to increase, successful pup rearing is critical. In this study, we determined the activity and energy budgets of sea otters in a prey rich area with little anthropogenic impact. By making detailed behavioral observations over a 24 hr period, we estimated the allocation of time and energy intake necessary for the female to sustain her health and that of the pup. These data provide additional information for understanding the population trajectories of sea otters in different geographic regions of the Pacific Ocean from northern Japan to Baja California.

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APPENDIX A

A-1. Female and pup sea otter behavioral states in Simpson Bay, Alaska.

Activity	**Mother**	**Pup**
Foraging for the female, feeding for the pup	Foraging dives to the benthos using simultaneous pelvic paddling to acquire food, handling/ingesting prey; includes dives and interdive intervals	Handling/ingesting captured prey or begging/stealing prey from the female
Nursing	Only recorded for pup	Pup suckling while laying on the female's abdomen or along side
Self-Grooming	Vigorous rubbing, licking, aerating own fur	Vigorous rubbing, licking, aerating own fur
Being Groomed	Only recorded for pup	Female vigorously rubbing, licking and aerating the pup's fur
Interacting	Interacting with any otter including the pup; Can be social or reproductive	Interacting with any otter including the female and other pups

APPENDIX B

B-1. Energy equivalents adapted from Thometz et al., 2014.

Activity	**Pup**	**Energetic Equivalent**		
		C1	**C2**	**C3**
Feeding	Handling/ingesting captured prey or begging/stealing prey from the female	Moderately Active	Moderately Active	Highly Active
Nursing	Pup suckling while laying on the female's abdomen or along side	Resting	Resting	Resting
Self-Grooming	Vigorous rubbing, licking, aerating own fur	2.2 x RMR	2.2 x RMR	2.2 x RMR
Being Groomed	Female vigorously rubbing, licking and aerating the pup's fur	Resting	Resting	Resting
Interacting	Interacting with any otter including the female and other pups	Moderately Active	Moderately Active	Moderately Active
Swimming	Generally occurs at the surface, paddling belly down; Older pups begin using alternate pelvic paddling; Occasionally submerged swimming using simultaneous pelvic paddling	Moderately Active	Moderately Active	Highly Active
Resting	Laying on females' abdomen; floating belly up motionless or with slight movement of forepaws, head or feet; hauled out; sleeping	Resting	Resting	Resting

a. Highly active = rapidly moving in the dome; submerged swimming; rapidly swimming on the surface during in-water trials

APPENDIX C

C-1. Energy content of invertebrates eaten by sea otters in Simpson Bay, AK.

Species	Sample Size	Mean wet weight	% water	EE values (MJ/Kg) dry weight	EE values (MJ/Kg) wet weight
Butter clam	139	10.21	84.59	19.46	3.00
Littleneck clam	49	4.05	84.09	19.37	3.08
Blue mussel	30	0.69	83.02	18.31	3.11
Sweet potato sea cucumber	24	10.29	77.45	6.86	1.55
Astarte sp.	20	1.27	79.73	19.68	3.99
Tanner crab	14	14.34	84.53	21.55	3.33
Red sea cucumber	1	120.35	82.13	19.69	3.52
Purple sea star	1	87.77	78.38	10.42	2.25
Mottled star	2	40.2 & 6.3	72.30	5.80	1.61
Alaska falsejingle	27	4.62	79.26	21.72	4.50
Fat innkeeper worm	5 (pooled)	-	97.26	18.43	0.50

APPENDIX D

D-1. Fat reserves in pregnant or lactating females from Kachemak Bay, Alaska. a) Renal fat b) Mesenteric fat.